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Investigation of natural patterns of coral recruit-benthos interactions with a focus on interactions with crustose coralline algae in Moorea, French Polynesia

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Faculdade de Ciências e Tecnologia

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Declaração de autoria de trabalho

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Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

(Clément Esclavy)

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Acknowledgment

I would like to thank Claire Boitel, Nour Bocquet, Clara Mantovani, Tuiterai Salmon and Eloise Deshaies for their support and help.

I would also like to thank Maggy Nugues for her exceptional expertise and invaluable collaboration in collecting data in the field, which greatly enriched this study.

My thanks also to Franck and Guillaume Iwankow for their essential role in ensuring safety on the surface during the multiple dives carried out.

Abstract

Crustose coralline algae and macroalgae play a vital role in the coral reef ecosystem by engaging in intricate relationships with corals. It is widely recognized that corals and crustose coralline algae (CCA) can form associations that have the potential to be beneficial for both the corals and the entire reef ecosystem. However, these relationships are often intricate and can be challenging to ascertain due to their subtlety. Because of the importance of CCA in coral reefs, there is growing interest in understanding their interactions with corals, in particular at the recruit life stage, although these relationships remain relatively undocumented and require specialist expertise.

In the context of this study, we conducted an in-situ survey at two distinct sites on the island of Moorea, namely Rotui and Temae. The objective of this research was to explore the type and outcomes of interactions between coral recruits and algae, with a focus on crustose coralline algae.

All non-cryptic CCA species exhibited neutral associations with corals, with predominantly negative outcomes on both study sites. *Porolithon onkodes*, a CCA, primarily displayed neutral interactions with coral recruits, although a negative percentage was recorded, positioning it as the less favorable CCA in these interactions. Additionally, more negative outcomes were identified for this CCA concerning small recruits (< 5 mm).

Cryptic CCAs, in contrast, demonstrated significantly more positive interactions, displaying a substantial quantity of positive associations with coral recruits. This was observed along with positive outcomes with *Harveylithon munitum, Mastophora Pacifica*, and CCA species CCA species forming thin crusts, with some variations between the two study sites.

Algae of the *Peyssonnelia* genus, the only non-calcareous macroalgae studied, exhibited no detrimental interactions with corals. Instead, they showed a considerable number of positive associations with coral recruits and were highly preferred by recruits under 5 mm.

The results of this study reveal the patterns of species-specific associations between CCAs and coral recruits in Moorea, while confirming the conclusions of previous studies on the interactions between corals and macroalgae. This makes it possible to determine which organisms promote successful coral recruitment and to identify those likely to alter the associations between corals and coralline algae, by inhibiting or hindering the recruitment of coral larvae.

Keywords

Moorea; Corals larvae ; Corals recruitment ; CCA ; Associations and interactions ; Macroalgae

Portuguese abstract

As algas coralinas encrustantes e as macroalgas desempenham um papel essencial e complexo no ecossistema dos recifes de coral, graças às suas interações intimamente entrelaçadas com os corais. É amplamente aceito na comunidade científica que os corais e as algas coralinas encrustantes (ACC) têm a capacidade de estabelecer associações potencialmente benéficas, contribuindo tanto para a vitalidade dos corais quanto para a integridade geral do ecossistema de recife. No entanto, é crucial notar que essas relações, devido à sua subtileza, são frequentemente difíceis de discernir. Devido à importância crucial das algas coralinas encrustantes nos recifes de coral, observa-se um aumento significativo do interesse na compreensão de suas interações com os corais. No entanto, é essencial destacar que essas relações permanecem relativamente subexploradas, e seu estudo exige especialização.

Como parte do presente estudo, realizámos vários levantamentos *in situ*, combinando observações de campo e análises laboratoriais, concentrando-nos especificamente em dois locais distintos na ilha de Moorea, nomeadamente Rotui e Temae. O principal objetivo foi obter uma compreensão abrangente dos padrões de associação entre corais e CCAs.

Em paralelle, a avalia do recrutamento de larvas de corais nessas associações e a examinação minuciosa das interações complexas entre os corais e as macroalgas foi feita. Esta abordagem permitiu uma compreensão mais aprofundada da dinâmica destas associações cruciais no ecossistema de recifes locais.

Essa abordagem meticulosa possibilitou a obtenção de uma compreensão mais abrangente e aprofundada da dinâmica dessas associações cruciais no ecossistema de recife de coral. Tal compreensão não apenas destaca a complexidade dessas interações, mas também ressalta sua importância crucial para os esforços de conservação e gestão dos recifes de coral, ecossistemas que se encontram altamente vulneráveis. O conhecimento aprofundado adquirido por meio dessa análise é fundamental para orientar estratégias eficazes que visem preservar a saúde e a resiliência desses ambientes marinhos essenciais.

Para este objetivo ser alcançado de forma abrangente, várias séries de investigações foram executadas, implementando uma variedade de métodos. Entre estes, a utilização de quadrados e transectos ocupou uma posição central. Os quadrados foram cuidadosamente posicionados para delimitar com precisão a área de estudo onde as recrutas coralinas estavam presentes, permitindo assim uma quantificação rigorosa da taxa de recrutamento dos corais.

Além disso, durante essas operações, dados foram meticulosamente coletados para registrar as associações entre os corais e outros organismos presentes nesse ambiente marinho complexo. Essas informações detalhadas são de importância crucial para a investigação dos padrões de associações e interações dos organismos bênticos com as recrutas de coral nos ecossistemas de recifes.

Ao mesmo tempo, os transectos foram cuidadosamente estabelecidos para avaliar a porcentagem de cobertura bêntica pelos diversos organismos do recife. Essa avaliação proporcionou uma perspectiva abrangente da composição do substrato bêntico e sua distribuição, fornecendo assim informações vitais sobre a saúde geral dos locais de estudo. A utilização de varios indicadores permitiu obter uma visão holística das condições ambientais e de seu impacto potencial sobre os organismos recifais.

Além disso, esses transectos desempenharam um papel fundamental na avaliação dos possíveis impactos nas interações bióticas dos organismos recifais. Essa abordagem permitiu observar de perto as dinâmicas complexas subjacentes às associações dentro desses ecossistemas frágeis. Em resumo, esta pesquisa rigorosa contribuiu significativamente para nossa compreensão das relações complexas que unem os corais e os organismos do recife, bem como para a identificação dos potenciais fatores que influenciam essas interações.

A grande maioria das espécies de algas coralinas encrustantes, não sendo crípticas, forão observadas formando associações geralmente neutras com os corais. É essencial notar que a natureza específica desses benefícios pode variar de acordo com os locais de estudo. Por outro lado, o ACC *Porolithon onkodes* foi identificado como a espécie de ACC que apresenta os resultados mais negativos para as recrutas de coral nos dois locais do estudo. Em contraste, as espécies de ACC crípticas exibiram resultados claramente mais positivos, especialmente espécies como *Mastophora pacifica* e *Harveylithon minutum*, assim como as espécies de ACC de camada fina. No entanto, é relevante notar que variações foram observadas entre os locais de Rotui e Temae em relação aos resultados das associações e interações entre esses organismos.

Uma observação particularmente interessante incide sobre as macroalgas, particularemente as espécies do género *Peyssonnelia*. Apesar uma incapacidade de produzir carbonato de cálcio, destacam-se pela notável ausência de resultados negativos de interação com os recrutas de coral. Mais ainda, os registos mostram que estabeleceram um número significativo de associações positivas com corais jovens, favorecendo estabelecimento e sobrevivência. Em contrapartida, as interacções da alga *Lobophora* com os recrutas de coral

revelaram uma maior proporção de resultados negativos entre as macroalgas. Entre as macroalgas examinadas, os resultados das interacções negativas foram induzidos por várias acções, algumas sendo mais comuns: a cobertura, a obstrução da luz e as interacções através de metabolitos secundários, fenómenos partilhados por várias espécies de macroalgas.

Os resultados deste estudo fornecem informações adicionais sobre os padrões de associação entre os ACC e os jovens corais de Moorea. Além disso, eles reforçam as conclusões anteriormente emitidas sobre os resultados das interações entre os corais e as macroalgas. Essa compreensão aprofundada permite identificar os organismos que favorecem o sucesso do recrutamento dos corais, destacando aqueles que podem potencialmente perturbar as associações entre os corais e as algas coralinas ao interferir ou obstruir o recrutamento de larvas de corais.

Essa análise aprofundada é de importância significativa para nossa compreensão dos ecossistemas de recife, e contribui de maneira crucial para a formulação de estratégias de conservação e gestão específicas adaptadas às necessidades desses ecossistemas de recife vulneráveis.

Palavras-chave

Moorea; Larvas de coral; Recrutamento de coral; CCA; Associações e interacções; Macroalgas

Table of content

List of Abbreviations, acronyms and symbols

Corals
ACR/Acr - Acropora
POC/Poc - Pocillopora
OTH/Oth - Other
Hc - Other corals (Acropora; Pocillopora; Other corals; Fire corals)
Fc - Fire corals
CW - Coral Win
CL - Coral Losses

Macroalgae
HighTF - High Turf
LowTF - Low Turf
Lob - Lobophora
Turb - Turbinaria
Hal - Halimeda
Dic - Dictyota
Asp - Aspagaropsis
OthMa - Other Macroalgae
Peys - Peysonnelids

CCA
Ponk - Porolithon cf. onkodes
Othporo - Porolithon spp.
Lins - Lithophyllum insipidium
Lfla - Lithophyllum flavescens
Mpul - Mesophyllum cf. pulchrum/erubescens
Dcon - Dawsoniolithon conicum/spp.
Nmeg - Neogoniolithon sp2 cf megalocystum
Hsp1 - Hydrolithon sp1
tkCCA - thick CCA
Mpac - Mastophora pacifica
Lsp3 - Lithophyllum sp3
Hmun - Harveylithon munitum/Spongites spp.
tnCCA - thin CCA

Other2 (OT)
Sp - Sponges
Bry - Bryozoans
Sd - Sand

1. Introduction

1.1 Complexity of coral reef ecosystems

Coral reefs, despite their relatively low occupancy in the ocean, covering approximately 0.2% of the total seafloor and a modest portion of shallow waters (0-30m) (Knowlton and Jackson, 2008; Fisher et al., 2015; Jorissen et al., 2020) stand out due to their extraordinary ecological productivity. They harbor remarkable biological diversity, encompassing around 35% to 38% of global marine diversity. Corals, in particular, play a central role in this context by providing a structural framework that creates a multitude of habitats conducive to ecosystem biodiversity (Knowlton and Jackson, 2008; Fisher et al., 2015; Jorissen et al., 2020). This capacity is not exclusive to corals alone but extends to other benthic organisms, notably the Coralline Crustose Algae (CCA) (Reaka-Kudla et al., 1996). In total, more than 830,000 species contribute to the exceptional diversity of coral reefs worldwide (Fisher et al., 2015).

In addition to their abundant biodiversity, coral reefs play a crucial role by providing essential ecosystem services (Harrison and Booth, 2007; Salvat et al., 2008; Woodhead et al., 2019). One of these fundamental services is coastal protection for islands (Payri, 1987; Salvat et al., 2008), which not only reduces erosion but also helps mitigate disease spread while facilitating biodiversity and nutrient exchanges (Stoeckl et al., 2011). This protection enhances the resilience of adjacent ecosystems to coral reefs, including mangroves and seagrass beds. Furthermore, coral reefs are vital for fisheries, ensuring food security for numerous communities worldwide that rely on marine resources from reefs (Stoeckl et al., 2011; Woodhead et al., 2019). This significance is particularly pronounced in equatorial and sub-equatorial regions influenced by solar irradiance and aragonite saturation and temperature (Abrego et al., 2021), where coral reefs are present in the Indian, Pacific, and Indo-Pacific Oceans, are characterized by exceptional diversity. Reefs are also found in the Atlantic, along the coasts of South America, and in the Caribbean.

The reef ecosystem is a highly complex system (Morrow et al., 2016) due to the numerous biotic interactions among reef organisms, contributing significantly to its complexity (Pawlik et al., 2007). More specifically, the vitality of coral ecosystems is based on interactions between among various essential benthic organisms, including corals, coralline crustose algae, macroalgae, and herbivores (Heyward and Negri, 1999; Negri et al., 2001; Harrington et al., 2004; Rasher and Hay, 2010; O'Leary et al., 2012; Smith et al., 2016). These interactions are of paramount importance for the equilibrium of the reef ecosystem. Coral recruits and established corals interact with a multitude of other reef organisms. For instance, coral recruits can form associations with coralline crustose algae (Dethier, 1994; Harrington et al., 2004; Heyward and Negri, 1999; Smith et al., 2016). Furthermore, coral recruits may interact with non-calcifying macroalgae (Stiger and Payri, 1999; Rasher and Hay, 2010; Vieira, 2020). Herbivores, such as fish, also play a fundamental role in these interactions by regulating macroalgae presence, indirectly impacting coral health. This regulation by herbivores is crucial (McCook et al., 2001; Rasher and Hay, 2010), because a decrease in herbivore populations can lead to a reduction in the coral population. Thus, the preservation of these complex interactions is of great importance for the health and sustainability of coral reefs.

1.2 Relationship between coral larvae, recruits and crustose coralline algae (CCA)

The majority of reef-building scleractinian corals (E/ Cnidaria, C/ Anthozoa SC/ Hexacorallia, O/ Scleractinia) have a larval phase in their life cycle. Coral larvae have a shape that differs depending on the taxon (Gleason and Hofmann, 2011), are composed of cilia and are able to swim in the water column (Morse et al., 1996). There are several modes of coral reproduction, but two are dominant: the broadcasting species type, consisting of the release of eggs and sperm into the water column, and the brooding species type, with the release of sperm into the water column and the incubation of the eggs in the polyp until the mature larval stage (Gleason and Hofmann, 2011). The larval stage is essential as it enables the dispersion of corals, promoting genetic diversity by larvae colonizing new habitats. When larvae approach the reef substrate, they are guided by signals emitted by Coralline Crustose Algae with which they maintain a complex yet fundamental relationship. These algae constitute an essential benthic functional groups for the functioning of reef ecosystems (Fabricius and De'ath, 2001; Harrington et al., 2004; Littler and Littler, 2013; Siboni et al., 2020).

Throughout the settlement phase, planula larvae are influenced by diverse chemical, physical and ecological signals (see review by Gleason and Hofmann, 2011). Among them, positive signals are generated by certain species of CCA (Heyward and Negri, 1999; Negri et al., 2001; Littler and Littler, 2013; Quinlan et al., 2019; Siboni et al., 2020). These signals guide coral larvae to settle in locations favorable for their survival, thereby enhancing post-settlement survival (Harrington et al., 2004; Smith et al., 2016). A significant species richness of coralline crustose algae (Rhodophyta, Family: Corallinaceae) is present on coral reefs, and these algae, also known as "CCA," play a key role in the reefs. These coralline algae are found in all oceans around the world and exhibit the highest diversity in tropical regions, extending to considerable depths, including the full range of organisms in the photic zone (Dethier, 1994; Littler and Littler, 2013).

Coralline algae have distinct ecological preferences, influenced by physical and biological factors such as water currents and herbivory. For example, some species thrive in lagoonal environments, while others prefer habitats characterised by more turbulent conditions, such as the reef crest and outer reef slopes, with depth also playing an important role in their species distribution (Harrington et al., 2004; Smith et al., 2016). These red algae grow in superimposed layers of cells with a calcified skeleton composed of calcium carbonate (CaCO3) (Heyward and Negri, 1999), forming a natural cement that helps to consolidate the reefs. These CCAs form surfaces that follow the topography of the reef seabed, providing a favourable base for anchoring organisms, particularly coral larvae (Fabricius and De'ath, 2001; Arnold and Steneck, 2011; Littler and Littler, 2013; Tebben et al., 2015; Yang et al., 2021).

Throughout the literature, this selection and settlement via signals (Heyward and Negri, 1999) remains partially understood because this installation mechanism via chemical signals may involve signals produced by the algae themselves or by algal-associated bacteria. Cellular compounds such as a specific morphogenic molecule present in the cell membrane of crustose coralline algae can also induce coral larval settlement (Morse and Morse, 1991; Raimondi and Morse, 2000; Quinlan et al., 2019). However, the bacterial communities present on CCAs can also induce coral settlement and these communities are thought to be CCA species-specific (Siboni et al., 2020), potential resulting in complex interactions with corals.

Associations between corals and certain species of CCA seem to show benefits for the former, as it has been established that certain species of CCA are associated with abundant coral cover and high densities of coral recruits (Dethier, 1994; Harrington et al., 2004; Littler and Littler, 2013). These benefits include inducing corals to settle, induction of coral metamorphosis, and increased survival following settlement (Arnold and Steneck, 2011; Abdul Wahab et al., 2023). This improved survival capacity is important, particularly given the constant competition that corals face from other organisms. In addition, larvae behave in ways that can be complex in response to biotic and abiotic factors (Price, 2010; Gleason and Hofmann, 2011).

Thus, CCAs are thought to be beneficial for larvae and young coral recruits during the initial phases of their development, as they are sensitive to variations in their environment, its fluctuations and the organisms living there (Arnold and Steneck, 2011). These coral recruits are a central pillar of reef dynamics and will eventually become the architects of these ecosystems. Most coralline algae are beneficial to coral recruits. Still some species may simply be neutral or even hostile to corals (Quinlan et al., 2019). Not all coralline species are beneficial to coral larvae, and some have defence mechanisms against the settlement of coral larvae (Harrington et al., 2004). CCAs use a wide variety of anti-settlement mechanisms. Most CCAs are capable of renewing their surface cell layer by epithelial excretion, this is the exfoliation (Keats et al., 1997b; Harrington et al., 2004). This corresponds to the 'anti-fouling' defense mechanisms that directly inhibit the recruitment of larvae to the surface (Keats et al. 1997b; Harrington et al. 2004). Some CCA species can also chemically deter corals from settling on their surfaces (Harrington et al. 2004).

Finally, although some CCA species are beneficial to corals, certain CCA species may compete with corals for space (Jorissen et al., 2020). This is also the case of many species of macroalgae.

1.3. Macroalgae in the Reef Ecosystem: Morphology, Ecological Role, Impact on Corals, and Ecological Interactions

Macroalgae are an important component of reef ecosystems. A large number of different macroalgae can be found, including the genera *Lobophora*, *Turbinaria, Halimeda, Asparagopsis, Dictyota* and *Peyssonnelia*, which are present in varying quantities depending on the state of the reef. The macroalgae *Asparagopsis*, *Dictyota*, *Turbinaria* (Longo and Hay, 2017) and *Lobophora* (Mumby et al., 2016) are among the most common algae in Moorea.

The algae of the genus *Lobophora* (F/ Dictyotaceae) are common brown algae that make up the world's temperate and tropical marine flora (Morrow et al., 2016), consisting of a small, flat thallus (Klomjit et al., 2022). These algae grow 'in mats' on a wide range of substrate types, generally covering rocky substrates. For instance, in French Polynesia, a total of 37 different species of *Lobophora* have been identified, representing as much as 10% of the diversity of Polynesian algae (Vieira, 2020). This alga has an important ecological role to play in reefs, when its population is regulated, enabling the creation of habitats through its 'covering', which is used in particular by organisms such as juvenile fish and small marine organisms. In addition, *Lobophora* is thought to be able to limit herbivory via powerful secondary metabolites (Morrow et al., 2016).

The species *Turbinaria ornata* (Sargassaceae) (Stiger and Payri, 1999) is a brown alga found in large quantities on the reefs of Moorea. It is composed of a thallus with a base made up of branches composed of conceptacles. Thanks to its three-dimensional structure, *Turbinaria* helps to create habitats for numerous organisms on the reefs (Bittick et al., 2019).

The algae *Halimeda* (F/ Halimedaceae), *Asparagopis* (F/ Bonnemaisoniaceae) and *Dictyota* (F/ Dictyotaceae) (Theophilus et al., 2020) are respectively green, red and brown algae found in warm tropical zones. As *Halimeda* is composed of calcareous structures (CaC03) that make it rigid, this alga is a calcifying primary producer that contributes to the accretion of coral reefs (Hofmann et al., 2014; Smith et al., 2016). It will be included in this research, even though it is not strictly a non-calcified alga. The species *Asparagopsis taxiformis* forms a dark red thallus with dense, non-rigid branches in clumps. The genus *Dictyota* is found in many parts of the world in tropical areas (Bogaert et al., 2020) and is composed of distinct Y-shape thalli. Many species of this genus inhabit the reefs of Moorea. The *Peyssonnelia* alga is a red alga (Rhodophyta, F/ Peyssonneliaceae) present on the reefs of Moorea. It can be distinguished from CCAs by its chemical composition, as it is not composed of CaCO3, and physically by its membranous structure, which is more flexible than that of coralline algae, and thus unlike the latter, this alga does not contribute to the accretion of reefs. According to some studies, *Peyssonnelia* interact positively with corals (Harrington et al., 2004; Ritson-Williams et al., 2009).

In a healthy reef ecosystem, macroalgae can co-exist beneficially (or neutrally) with organisms such as corals and CCA, provided they are adequately regulated within that ecosystem (Smith, 2016). However, when reef health is impaired, reefs may experience a significant proliferation of macroalgae due to their ability to expand rapidly and excessively (Arnold and Steneck, 2011; Littler and Littler, 2013; Smith et al., 2016; Vieira, 2020). In such circumstances, the detrimental effects of algae on corals tend to outweigh their beneficial impacts (Bittick et al., 2019; Theophilus et al., 2020). In addition, certain macroalgae (particularly *Lobophora*) can inhibit coral recruitment and growth through several mechanisms, the main one being the production of primary and secondary metabolites that influence bacterial communities, creating competition with corals (Amsler, 2001; Baumgartner et al., 2009; Morrow et al., 2016).

A multitude of negative impacts can be exacerbated by the excessive proliferation of macroalgae, making these algae non-beneficial organisms for corals and potentially altering coral recruitment and survival. Direct competition for space (Jorissen et al., 2020) and light blockage (McCook et al., 2001) are the main negative impacts macroalgae can have on corals and other reef organisms.

1.4. Aim of the study: Study of the Associations and Interactions outcomes between Coral Recruits and CCAs and Macroalgae

The primary goal of this study is to unravel the patterns of association between young corals and Crustose Coralline Algae (CCA), as well as their interactions with non-calcifying macroalgae within two reefs on Moorea Island, namely Rotui and Temae. These reefs exhibit distinct health conditions, providing a comprehensive assessment of coral recruitment, environmental influences, and overall reef health. To achieve this, we have employed various methodologies, with a specific focus on coral recruits measuring less than 30 mm in size. Our research aims to deepen our understanding of the intricate relationships that exist within reef ecosystems.

It is noteworthy that research on specific species of coralline algae in French Polynesia remains limited, with the majority of studies conducted in Caribbean reefs and the Great Barrier Reef in Australia. Furthermore, by examining interactions between corals and non-calcifying macroalgae, including those present in substantial quantities, we can gain a more comprehensive understanding of coral relationships with a variety of organisms, extending beyond CCA alone. This approach enables us to better comprehend the complex interactions governing life on coral reefs.

Importantly, French Polynesian reefs face numerous disturbances, primarily from climate change-induced heatwaves resulting in increasingly frequent bleaching events. These events leave coral structures dead, allowing macroalgae to proliferate rapidly, leading to a high abundance of fleshy macroalgae that degrade reef health. Some reefs experiencing such massive macroalgae proliferation undergo a phase shift, where the proportion of coral cover is significantly reduced in favor of non-calcifying macroalgae. Several other disturbances, such as outbreaks of *Acanthaster planci* (crown-of-thorns starfish) and overfishing, also contribute to significant damage to coral communities. The cumulative impact of all these disturbances brings about substantial changes in the interactions between corals and reef organisms that play a critical role in maintaining reef health.

Hence, it is imperative to measure coral recruitment rates and quantify coral cover to gain insights into the health trends of the studied sites. This study allows us to monitor the evolution of these relationships across reefs with varying degrees of impact from these disturbances.

In the field survey, we employed quadrat methodology to measure coral recruitment and evaluate the types and outcomes of interactions at each site. Identification of coral recruits and organisms was primarily conducted in situ using specialized equipment, with laboratory procedures used as needed. Percentage cover measurements were carried out through transects at both study sites. Two hypotheses emerge from this study. First, it is suggested that the patterns of associations between corals and CCA may vary, implying that certain CCA may provide more favorable association patterns for corals than others. Second, it is hypothesized that non-calcifying macroalgae could have an overall detrimental impact on corals, especially due to their ability to rapidly colonize an area, particularly after disturbances, and potential adverse interactions with corals (Vieira, 2020).

Addressing these gaps in our understanding of reef ecosystems is crucial for developing tailored management plans and optimizing the preservation of these invaluable habitats. By obtaining a comprehensive and in-depth understanding of the dynamics and relationships between corals and other reef organisms, we will be better equipped to implement more effective conservation measures. Thus, this study aims to shed light on the intricate interactions shaping life on the coral reefs of French Polynesia and contribute to the preservation of these unique and vulnerable ecosystems.

2. Materials and Methods

2.1. Study sites

Moorea (17°32' S; 149°49' W) is an island in French Polynesia located in the Pacific Ocean, within one of the five archipelagos of Polynesia, the Society Islands (Isles of the Society). Moorea is characterized by a fringing reef along its shores, followed by a lagoon leading to the barrier reef, known as the reef ridge, and ending with the outer slope (Salvat et al., 2008) (Fig. 1.b). The reef crest plays a crucial role in protecting the island from wave action, serving as a natural barrier that mitigates the impact of waves originating from the open sea. It also facilitates the exchange of water between the open ocean and the lagoon, thereby enhancing the connection between coastal and marine ecosystems. This is primarily accomplished through the presence of eleven passes encircling the island (Galzin & Pointier, 1985). The study was conducted at two distinct sites, referred to as Rotui and Temae, located in the northern (17° 28.582'S 149°50.696'W) and eastern (17° 30.381'S 149° 45.569'W) regions of Moorea, respectively (Fig. 1.A).

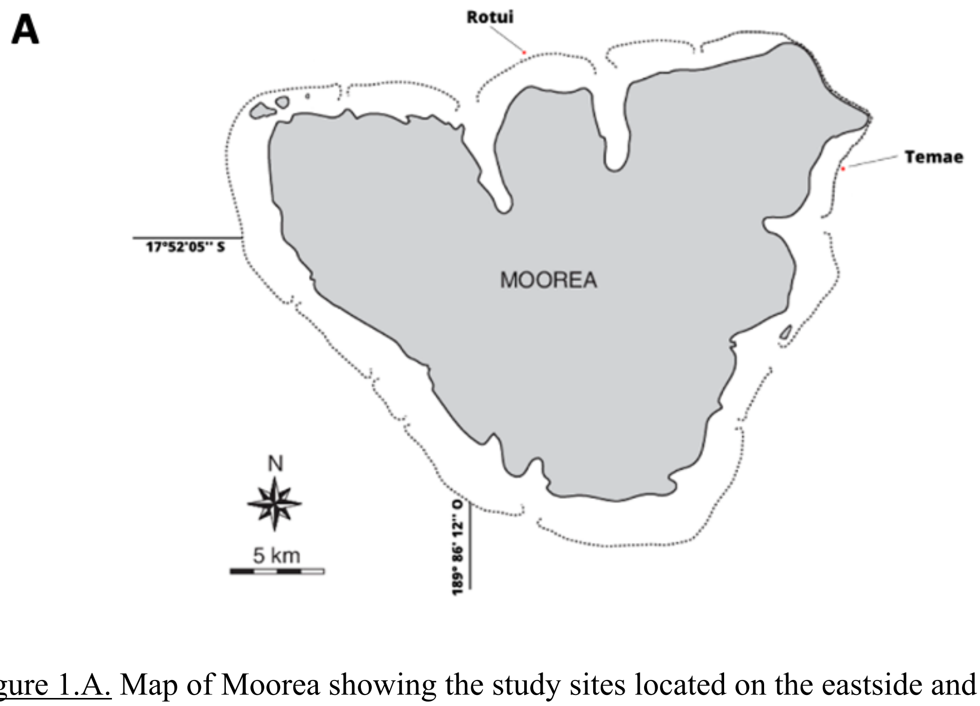


Figure 1.A. Map of Moorea showing the study sites located on the eastside and northside on the external slope, red points represent the exact location of those sites (Carroll et Al., 2016).

The selected study sites were located on the outer slope (the seaward side of the lagoon) to maximize coral, CCA (Coralline Algae), and organism diversity, which is greater what can be found in the lagoon. These sites were chosen based on their distinct locations and varying health conditions. For instance, the Rotui site has exhibited signs of coral community decline in recent years (Fig. S2) whereas Temae is in a comparatively healthier state (Fig. S2). Additionally, the two sites differed slightly in their topography, with Rotui featuring more cryptic areas, while the Temae terrain was flatter. The Rotui study site is located at the summit of one of the submerged lava fingers of Moorea, flanked by sand patches on both sides. It is characterized by steep drop-offs, with a descent of approximately 10 meters from the finger's pinnacle to its base. This configuration provided a substantial study area, with depths ranging from 9 meters at the finger's apex to 13 meters at its edges. In contrast, the Temae site displayed less relief, featuring a gentle slope extending from the reef crest to the outer slope. The depths of both study sites were similar, ranging from 10 to a maximum of 12 meters.

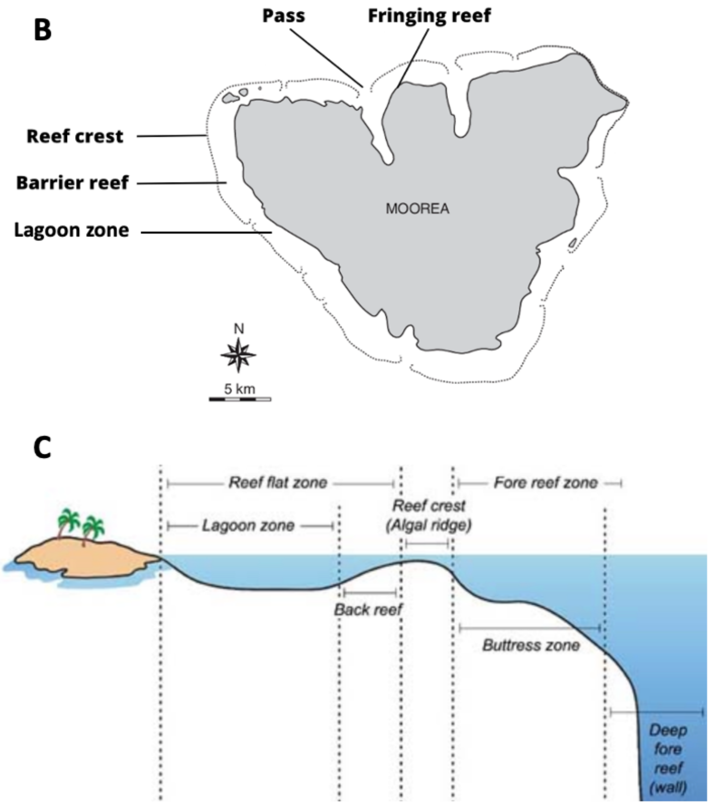


Figure 1.B.C. B) Map of Moorea showing the reef components of the island (Carroll et Al., 2016). C) Coral reef profile showing the different zones and their characteristics on a general coral reef (NOAA).

2.2. Study design and protocol

A. Interactions of coral recruits with adjacent organisms

In order to study the interactions between coral recruits and the organisms in contact with them, a total of 70 quadrats measuring 1 square meter were deployed to delimit the search zone for coral recruits (Tab. S1 and Tab. S2). The quadrats were randomly placed in various zones within each site, independent of the other survey (transects), at depths ranging from 9 to 12 meters. These were chosen to be no larger than 30 mm, so that they would not be older than 2 years. The minimum size of recruits was 1 to 2 mm, corresponding to ca. 3-month-old recruits.

Coral recruits were categorized according to their genera when identifiable, due to their small size. Species identification is not always possible at this size, as morphological features were not fully developed. We decided to focus on *Acropora* and *Pocillopora* genera as they are more easily identifiable, make up most of the coral cover on the outer reef (Fig. S3) at both sites and are of great ecological value as they provide important shelter for fishes within their branches later on as adults. Recruits from other genera, such as *Montipora*, *Porites*, *Psammocora* or *Leptoseris* for example, have been classified in the "Other" category (Oth).

On the other end, some CCA could be identified to the species level in situ, such as *Porolithon onkodes, Lithophyllum insipidium, Lithophyllum flavescens, Mesophyllum pulchrum, Dawsoniolithon conicum, Neogoniolithon megalocystum, Hydrolithon sp.1. Mastophora pacifica, Lithophyllum sp.3, Harveylithon minutum*, while others whose identification to species was complex where categorized to the genus level, such as *Porolithon spp*. and thin and thick coralline species.

For each coral recruit, the outcome of the interactions (negative, neutral and positive) with each organism was recorded following the methodology of Barott et al. (2012). The identification of the interaction was determined in relation to the organism that overlapped the other. In this case, the organism above is the 'winner' while the one overlapped is the 'loser' of the interaction, as illustrated in figure S.2 (e.g. *Lobophora* on a coral).

A total of 462 coral recruits were recorded, with the nature of the coral recruit-organism interactions indicated for each of them, as well as their size, genus when possible and depth. The interactions recorded provided a general overview of the preferential or avoidance interactions between the recruits and neighbouring organisms (Fig. 5). Most notably, the outcome of the interactions between corals and CCA or, non-calcarous macroalgae was identified (Fig. 5; Fig. 6 and Fig. 7). The data recorded via the quadrats were used to estimate the density of coral recruits per square meter for each site and genus (Fig.3). This allowed to give an idea of the quality of recruitment at each site (amount of recruits and distribution of genera).

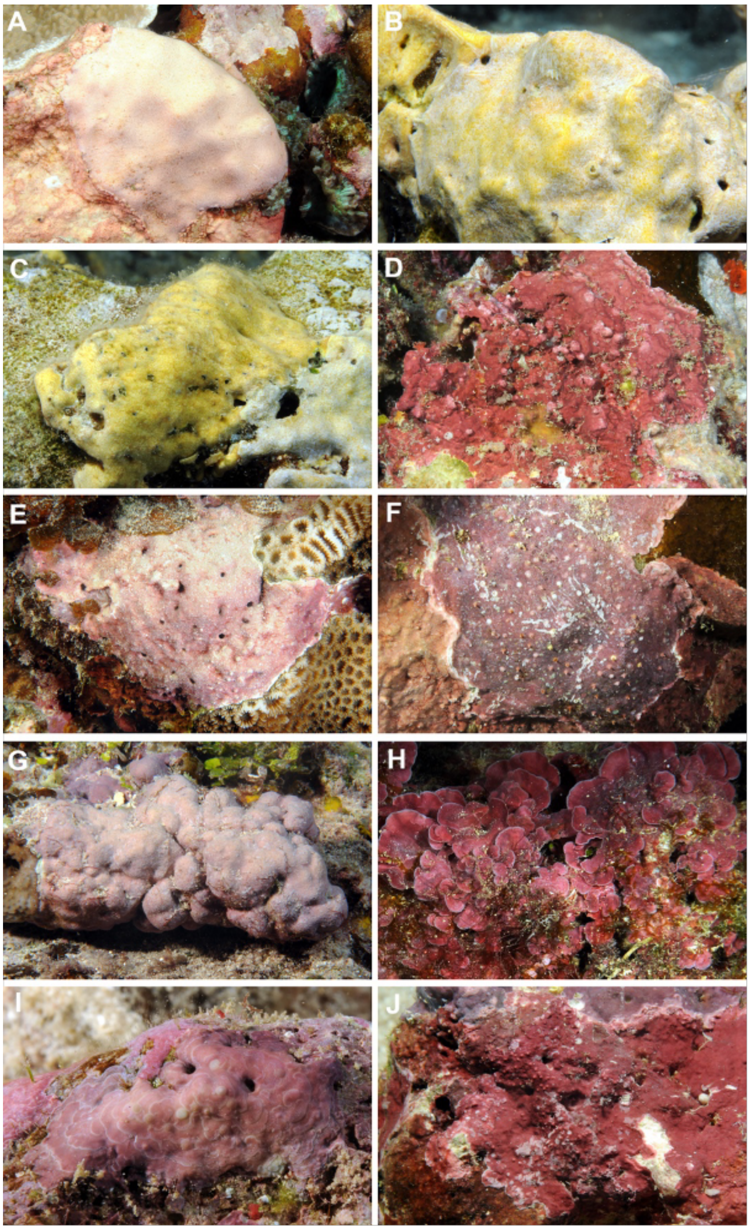


Figure 2. In situ photographs of representative crustose coralline algal morphotype used in this study. A) Porolithon onkodes. B) Lithophyllum insipidium. C) Lithophyllum flavescens. D) Mesophyllum pulchrum. E) Dawsoniolithon conicum. F) Neogoniolithon megalocystum. G) Hydrolithon sp.1. H) Mastophora pacifica. I) Lithophyllum sp.3. J) Harveylithon minutum. (Photos : Maggy Nugues)

B. Benthic cover estimation

A total of 16 transects, in the form of 10-meter graduated stainless steel chains, were deployed on the benthos to collect benthic cover data at the two distinct study sites (Fig. 4). These 16 transects were evenly distributed between the two sites (8 transects per site) and yielded data on the proportions of organisms present on both reefs. This data provided insights into the site health and the biotic factors which could influence the interactions between corals and organisms. The transects were placed at random on each of the 2 sites parallel to the coastline. Measurements were conducted in centimeters over a 10-meter span per transect. The method consisted of measuring the lengths of each organism under the chain from end to end. Organisms were classified into the same 29 categories as used for the quadrats.

2.3. Sample collection and processing

Samples were collected in quadrats and transects when identification was uncertain or complex to determine in situ, requiring more in-depth expertise with equipment that allowed greater precision (Quinlan et al., 2019). Hammers and chisels were used to collect the organisms, and the samples were then placed in resealable bags with a number corresponding to the quadrat being analysed. In the laboratory, the samples with the recruit (sometimes several) and the organisms bordering it were rinsed in fresh water for 1 minute, then placed in an drying oven at 60°C for 1 day and classified according to the same numbering as the bags. Analyses using 2 binocular magnifying glasses (Leica EZ4 HD and Stemi 2000-C) were used to identify certain coral species, as well as organisms in contact with the recruits, such as coralline algae, which are sometimes difficult to identify to species level in the field. Here again, the percentage of organisms was estimated around the recruits collected.

A study on the genetics of coralline species (CCA) carried out by Claude Payri in collaboration with Maggy Nugues in 2021 identified the coralline species of French Polynesia. A total of 35 CCA species and 17 morphotypes were established. During identification, some CCA species were identified to the genus, as identification to the precise species was too uncertain.

2.4. Data Analysis

All statistical analyses were performed using R Version 2023.06.0+421.

2.4.1. Recruit density and interactions between coral recruits and other organisms

Statistical analysis-was carried out on a total of 462 recruits. As previously stated, the assessment of coral recruit density by site (Rotui and Temae) and by genera Acropora, Pocillopora and Other corals was carried out. The data collected were-counts consisting of many values equal to 0.

The effects of sites and genus were determined using a Generalized Linear Model (GLM) fitted with a Poisson distribution (log link) commonly used for count data. Goodness-of-fit of models was evaluated with the "DHARMa" package (Hartig 2019; Fig S4). Overdispersion was corrected using a Negative Binomial distribution (package MASS; (Venables and Ripley, 2013)).

All models were fitted by performing type II Wald Chi-Squared tests, using the package "car" (Fox and Weisberg, 2018). It allowed to test for the significance of site, coral genera and their interaction. Estimates of the marginal means called "emmeans" were carried out (Package: emmeans) followed by a post-hoc t-test with Tukey correction to determine differences between coral genera.

The percentage of interactions for all coral recruits was calculated taking into account three conditions: "coral winner", "standoff", and "coral loser", based on the type of interactions (negative, neutral, and positive). At each of the 2 sites, the overall percentages for the 3 conditions were calculated as well as detailed coral-organism interactions for 12 categories of organisms which were chosen according to the amount of data collected for each organism (LowTF; HighTF; Peys; Lob; OthMa; Ponk; OthtkCCA – OthPoro, Lins, Lfla, Mpul, Dcon, Nmeg; Hsp1, tkCCA - ; Mpac; Hmun; OthtnCCA -Lsp3, tnCCA - ; Sp and Other - Bry; Sd and Hc -). Being able to categorize and count the different types of interactions will allowed to highlight beneficial and detrimental benthic organisms for coral recruitment.

2.4.2. Site characterization

For each site, the cover percentage of each category of organism was recorded over 10m (transect length). It was decided to consider only 20 categories of organisms, which were created from the 29 base organisms by associating certain organisms with others, in order to better visualise the categories most relevant to the study (LowTF; HighTF; Lob; OthMa; Ponk; OthPoro; Lins; Lfla; Mpul; Dcon; Nmeg; Hsp1; tkCCA; Mpac; Lsp3; Hmun; tnCCA; Peys; OT and HC). To give a better visual indication of the type of organism, color codes were used (dark green: Turfs; light green: other macroalgae; pink: CCA, dark pink: cryptic CCA, orange: *Peyssonnelia*; sand: Other (OT); blue: Other corals). Means and 95% confidence interval were calculated for each of the organisms represented.

To assess community composition differences between sites, Bray-Curtis dissimilarity matrices were computed (distances calculated between pairs of transects, with distances of 0 for transects sharing all taxa and 1 for transects sharing no taxa). Data were square-root transformed beforehand to reduce the influence of very abundant taxa (Beldade et al., 2015). To test for significant differences in composition, we first ran a Permutational Analysis of Multivariate Dispersion to check for homogeneity of dispersions between groups (999 permutations), followed by a Permutational Multivariate Analysis of Variance (PERMANOVA) on these dissimilarity matrices (999 permutations) with coral genera and sites in interaction (Topor et al., 2020) (Fig. S4).

Finally, a similarity percentage analysis (SIMPER) was used to assess which of the 20 categories of benthic organisms contributed most to the differences (overall dissimilarities) between sites. All analyses were carried out using 'vegan' software (Oksanen et al. 2022).2.4.3. Strauss' Linear selection Index

2.4.3. Strauss' Linear selection Index

The Strauss linear selection (L) index (Ivlev, 1961; Strauss, 1979; Mantyka and Bellwood, 2007; Madduppa et al., 2014) is defined by the following equation:

$$L = r_i - p_i$$

with r_i corresponding to the percentage of the total coral perimeter in contact with organism i (according to the study of coral recruitment carried out with quadrat survey) and p_i the percentage of coverage of organism i (according to the study carried out with transect survey).

In order to calculate an index L for each recruit, it was necessary to assume that the recruit was round-shaped in order to calculate the perimeter (approximated to a circle: p_i*diameter). The index values established ranged from -1 to 1, with positive values indicating a preference of the recruit for the adjacent organism and negative values an avoidance of the recruit for the adjacent organism (Madduppa et al., 2014). Coral recruits were divided into 3 size classes, <5 mm; 6 to 14 mm and 15 to 30 mm. These 3 classes make it possible to show the behaviour of the smallest recruits from the largest (the youngest and are more representative of the microenvironment where larvae settled). Values for each benthic category and each recruit size class were shown in order to visualize whether they are preferred by the recruits (part greater than 0), avoided (part less than 0) or neutral (interval passes through 0.0) (Mantyka and Bellwood, 2007). Since quadrats and transects were run independently, it was not possible to have replicated values and run statistical analysis on this index.

3. Results

3.1. Recruitment rates

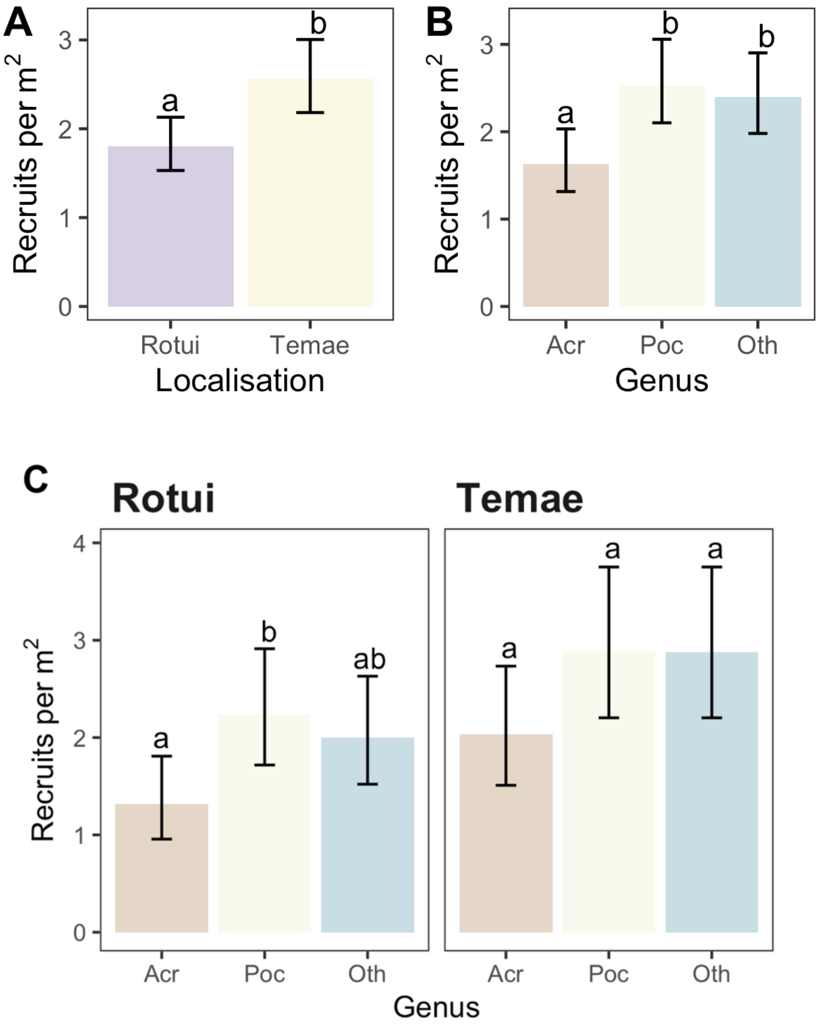


Figure 3. Estimated mean coral recruitment per square meter (quadrat) with error bars (asymptotic confidence intervals) as a function of study sites (A), the coral genera Acropora, Pocillopora and Other (B) and the combinations of study site x coral genera (C).

Coral recruitment rates were significantly different between sites (α= 0.05; p.value=0.0029), with on average a lower rate (1.8 recruits/m^2) for Rotui compared to Temae (2.6 recruits/m^2; Figure 3A). There was also a significant effect of coral genus, with *Acropora* recruits having lower recruitment rates than Pocillopora recruits and other corals. Significant differences between genus *Acropora* with genus *Pocillopora* and other coral genera were shown (α= 0.05; p.value(Acropora / Pocillopora) = 0.0077; p.value(Acropora / Other) = 0.0258; p.value(Pocillopora / Other) = 0.9116 (Fig. 3.B). At Rotui, *Acropora* recruits less (on average

1.3 recruits/m²) than the other genera (on average 2 recruits/m²) and *Pocillopora* (on average 2.25 recruits/m²). At this same site, a significant difference between the recruits of the *Acropora* genus and those of the *Pocillopora* genus was shown (α= 0.05; p.value(Acropora / Pocillopora = 0.032). The difference between *Acropora* and the other corals was not significant, and this was also the case between *Pocillopora* and Other (α= 0.05; p.value(Acropora / Other = 0.1239; p.value(Pocillopora / Other = 0.8327). Recruitment at Temae is different from that at Rotui, with a higher number of recruits per square metre for each of the 3 categories of coral genus (Acropora: 2 recruits/m2 ; Pocillopora: 2.8 recruits/m2 ; Other genera: 2.8 recruits/m2). At Temae, there was no significant effect of coral genera on recruit densities (α= 0.05; p.value(Acropora / Pocillopora = 0.2025; p.value(Acropora / Other = 0.2025 ; p.value(Pocillopora / Other =1.0000) (Fig. 3.C). Data are shown in Tab. S.1 and Tab. S.2.

3.2. Benthic cover

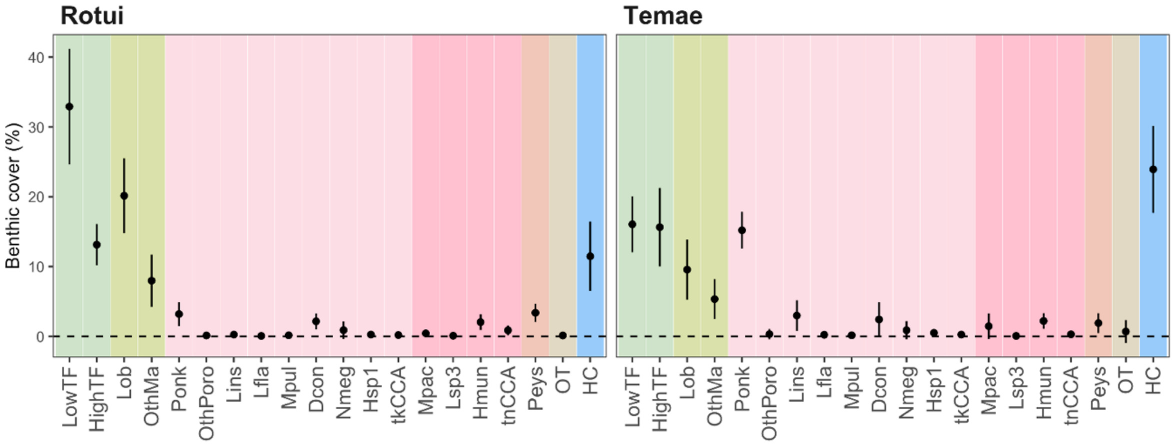
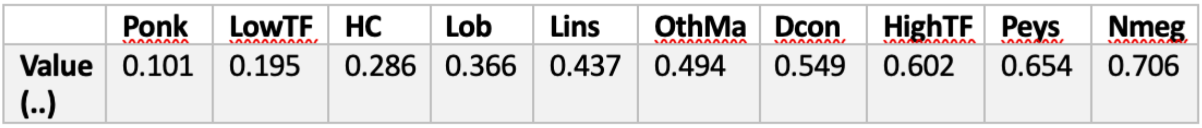


Figure 4. Percentage (mean ± SEM, 95% CI, n = 8 transects) of benthic coverage of the 20 categories of organisms at Rotui and Temae sites.

Benthic cover differs between sites, especially in terms of turf and macroalgal communities. Rotui had around 74% (Low Turf: 32.9 ± 8.3% / High Turf 13 ± 3% / Lob: 20.2 ± 5.4% / Other-Macroalgae: 8.0 ± 3.7%) of cover corresponding to algae. In Temae, the algae coverage accounted for a total of 46.5% (Low Turf: 16.1% ± 4% / High Turf: 15.5% ± 5.5% / Lob: 9.6% ± 4.3% / Other-Macroalgae: 5.3% ± 2.9%). The coverages of Low turf and *Lobophora* were twice as high at the Rotui site compared to Temae. In contrast, *Peyssonnelia* cover showed an opposite trend, it was present in smaller quantities than at Rotui, with a rate of 1.9%, compared to 3.4% at Temae (Figure 4). Likewise coral cover was two times lower at Rotui (11.5% ± 5%) than at Temae (23.9% ± 6.2%).

Globally, species of coralline algae were significantly more abundant in Temae, accounting for a total of 26.8%, compared to 9.8% in Rotui (Figure 4). Notably, *P. onkodes* is particularly prevalent at Temae, representing 15.2% ± 3%, in contrast to its scarce presence at Rotui, where it accounted for only 3.2% ± 1.7%, marking an approximately fivefold difference. Furthermore, the CCA *Lithophyllum insipidium* is primarily concentrated at Temae (2.9% ± 2.2%), whereas it is recorded in very low quantities at Rotui (0.25% ± 0.38%). The recorded rates for the crustose coralline algae *Harveylithon munitum* and *Dawsoniolithon conicum* are very similar between the two sites. At the Rotui site, the rate for *H. munitum* is 2% ± 1.1% compared to 2.1% ± 1.1% for *D. conicum*, and at the Temae site, values were 2.2% ± 1.2% and 2.4% ± 2.4%, respectively. The cover of *Mastophora pacificata* is slightly less than that of *H. munitum* and *D. conicum* for Temae with 1.5 ± 1.8% compared with 0.2% at Rotui. *Neogoniolithon sp2* (cf *N.megalocystum* (Nmeg)) has approximately the same coverage rate at Rotui and Temae (1 ± 0.8%). Other-CCAs such as *L. flavescens*, *M. pulchrum*, *H. sp1*, *L. sp3* and thick CCAs were rare, with a value close to 0 % at both sites.



	Ponk	**LowTF**	**HC**	**Lob**	**Lins**	**OthMa**	**Dcon**	**HighTF**	**Peys**	**Nmeg**
Value (..)	0.101	0.195	0.286	0.366	0.437	0.494	0.549	0.602	0.654	0.706

Table 1. SIMPER analysis : Contribution cumulative des 10 principales catégories d'organismes les plus influents à la dissimilarité entre les 2 sites

This table shows the analysis of dissimilarities using the SIMPER analysis method, between the most influential categories of organisms between the 2 sites among the organisms present on the benthos. Simper shows that *P. onkodes* is the most influential organism showing the greatest dissimilarity between the 2 sites. It is followed by Low turf algae and corals as well as *Lobophora*, which also show significant dissimilarity between the 2 sites.

3.3. Composition of the benthos interacting with coral recruits

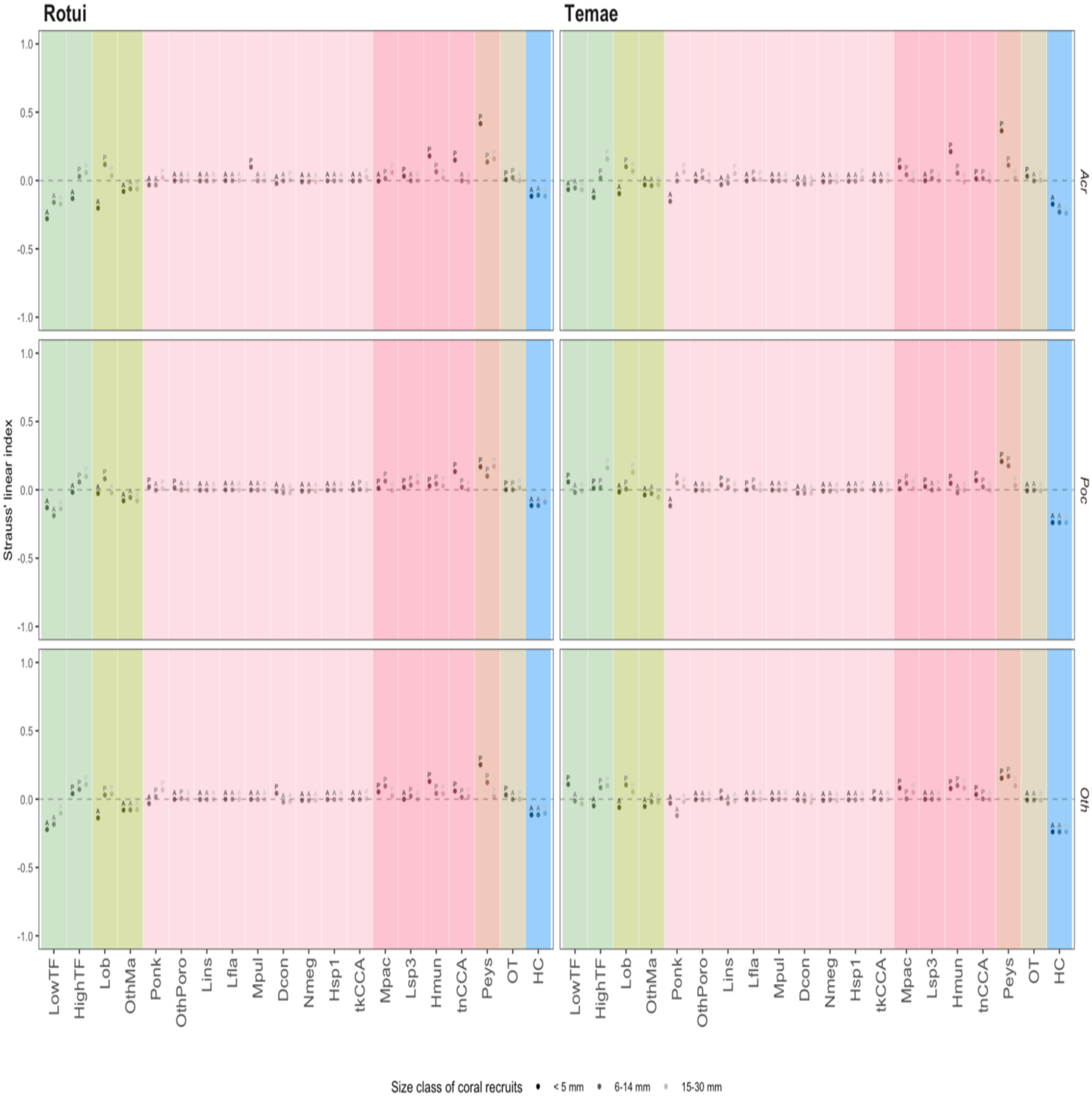


Figure 5. Strauss linear selectivity index for the 20 categories of organisms at Rotui and Temae sites for the 3 coral genera (Acr; Poc; Oth) and 3 classes of coral size (A: Avoidance; P: Preferences).

Macroalgae

Regarding the algae, the study revealed that the three coral genera tend to avoid low turf at Rotui, regardless of their size (Fig. 5.A). Conversely, at Temae, low turf seems to be better tolerated ($L > 0$), especially among the smallest recruits (those under 5 mm), with preferences observed for the Pocillopora and Other genera. The other size categories (6-14 mm and 15-30 mm) showed avoidance on both sites for all three coral genera.

Similarly, with high turf, corals from Temae exhibit a slightly higher level of tolerance, especially with the *Acropora* and *Pocillopora* genera, showing preferences for sizes 6-14 mm and 15-30 mm and for all three size classes, respectively. However, the Rotui site records preferences for all three size classes of the Other genus, with the most significant preference observed for the 15-30 mm size class, where Temae shows avoidance for recruits under 5 mm for this genus (Temae: (Oth) <5mm: [-0.048]), as well as for Acropora (Temae: (Acr) <5mm: [-0.123]).

On both study sites, *Lobophora* algae were notably avoided by recruits, especially by *Acropora*, which showed a trend of avoidance on both sites, particularly at Rotui (Rotui: (Acr) <5mm: [-0.201]; Temae: (Acr) <5mm: [-0.09]). Avoidance is shown by all coral genera with sizes less than 5 mm, the size class that seems to prefer this macroalgae concerns the intermediate size class (6-14 mm) for all coral genera on both sites. Overall, coral size classes over 5 mm appeared to avoid *Lobophora* algae less.

All size classes of recruits from all coral genera at both sites showed negative outcomes for Other macroalgae. However, on the Rotui site, slightly stronger avoidance for those algae is observed compared to the Temae site.

Encrusting red algae of the *Peyssonnelia* genus only showed positive outcomes with all three coral genera on both study sites, seeming to be more beneficial for the smallest coral recruits. This is evident, particularly with the *Acropora* and *Pocillopora* genera on both sites (Rotui: (Acr) <5 mm [0.416]; (Poc) <5 mm [0.168]; Temae: (Acr) <5 mm [0.364] (Poc) <5 mm [0.208]). Overall, all recruits seem to have a preference for this algae during their settlement. This preference is less pronounced for larger corals, especially on the Temae site for the *Acropora* and *Pocillopora* genera, where the preference is less significant than for the two smaller size classes. This trend is reversed for the Other genus corals on the Rotui site (Rotui: (Acr) 15-30mm: [0.158]; (Poc) 15-30mm: [0.171]; (Oth) 15-30mm: [0.018]; Temae: (Acr) 15-30mm: [0.017]; (Poc) 15-30mm: [0.031]; (Oth) 15-30mm: [0.098]).

Non cryptic CCA

First with coralline algae, the CCA *P. onkodes* presented mostly positive outcome on both sites, but it was more favored by recruits at the Rotui site. The three genera of coral recruits, belonging to size classes of 15-30 mm in all three coral genera, showed a preference, slightly more pronounced for the Other genus (Rotui: (Oth) 15-30 mm: [0.068]). A similar trend was observed in the 5 mm size class of the *Pocillopora* genus and the 6-14 mm size class of the Other genus (Rotui: (Poc) < 5 mm: [0.021]; (Oth) 6-14 mm: [0.018]). However, the Temae site showed a more negative trend among recruits, with more pronounced avoidances. Particularly, *Acropora* genus recruits in the 5 mm size class displayed a more negative outcome (Temae: (Acr) < 5 mm: [-0.152]), while larger-sized recruits exhibited more positive outcome (Temae: (Acr) 15-30 mm: [0.063]). Avoidance of *P. onkodes* was observed for all recruit sizes of the Other genus.

Other species of the *Porolithon* genus generally showed negative outcomes with recruits, except at Rotui for *Pocillopora* genus under 5 mm and Other genera measuring between 6 and 14 mm (Rotui: (Poc) < 5 mm: [0.014]; (Oth) 6-14 mm: [0.004]), the same trend was observed at Temae with *Acropora* of 6 to 14 mm (Temae: (Acr) 6-14 mm: [0.020]).

On the Rotui site, coral recruits displayed negative outcomes with the CCA *L. insipidium* and *L. flavescens*, regardless of their sizes. These CCAs are largely avoided at Temae. *L. insipidium* is preferred by *Pocillopora* and Other (5 mm) recruits, as well as *Acropora* (15-30 mm) recruits (Temae: (Poc) < 5 mm: [0.036]; Temae: (Oth) < 5 mm: [0.007]; (Temae: (Acr) 15-30 mm: [0.052]). As for the CCA *L. flavescens*, it is slightly preferred by recruits of the *Acropora* (15-30 mm) and *Pocillopora* (5 mm) genera, as well as the 6-14 mm sizes for these two coral genera (Temae: (Acr) 15-30 mm: [0.0068]; (Poc) < 5 mm: [0.0002]. (Acr) 6-14 mm: [0.009]; (Poc) 6-14 mm: [0.020]).

M.pulchrum is strongly avoided by all recruits, across all size classes, except for *Acropora* genus recruits smaller than 5 mm at Rotui (Rotui: (Acr) < 5 mm: [0.098]). *D.conicum* shows the same trend at the Temae site, where all size classes of recruits avoid the CCA, with slightly positive results at Rotui. *Acropora* (15-30 mm) and Other (5 mm) genus recruits are more strongly preferred on this site (Temae: (Acr) 15-30 mm: [0.003]; (Oth) < 5 mm: [0.042]). In contrast, the CCA *N.megalocystum* shows negative outcomes for all coral recruits on both study sites.

H.sp1 is avoided by all recruits at the Rotui site and shows preferences for larger-sized corals of the *Acropora* and *Pocillopora* genera at the Temae site (Temae: (Acr) 15-30 mm [0.020]; (Poc) 15-30 mm [0.002]). Concluding with non-cryptic CCAs, thick CCAs are avoided by Temae recruits, except for smaller-sized recruits of the Other genus (5 mm) (Temae: (Oth) < 5 mm [0.003]). A significant number of preferences are recorded at Rotui, especially for larger-sized recruits of the *Acropora* and Other genera (15-30 mm), as well as for *Pocillopora* recruits (6-14 mm) (Rotui: (Acr) 15-30 mm: [0.024]. (Oth) 15-30 mm: [0.0034]; (Poc) 6-14 mm: [0.0029]).

Cryptic CCA

Cryptic CCAs show significantly more positive outcomes in their preferences with recruits. The CCA *M.pacifica* exhibits positive outcome, preferred by all recruit sizes at the Temae site, more positive than at the Rotui site, where slight avoidances are found for larger-sized recruits of the *Pocillopora* genus and smaller-sized recruits of the *Acropora* genus (Rotui: (Poc) 15-30 mm [-0.0042]; (Acr) < 5 mm [-0.0042]).

All recruit size classes at Rotui show preferences for the CCA *H. munitum*. At Temae, preferences are observed for the Other genus in all size classes, however avoidances are noted for larger-sized recruits of the *Acropora* (Temae: (Acr) 15-30 mm [-0.0083]) and *Pocillopora* genera, with a 6-14 mm class showing avoidance (Temae: (Poc) 6-14 mm [-0.022]). *Acropora* genus recruits smaller than 5 mm, in particular, exhibit a clear preference for this CCA (Temae: (Acr) <5 mm [0.211]).

The outcome of ACC L.sp3 on coral recruits was more negative than the two previous CCAs, particularly at the Temae site, where avoidances for the Other genus are observed in all size classes. Similarly, avoidances are found for the *Pocillopora* genus, except for the smallest size class (Temae: (Poc) <5 mm [0.023]). Moreover, a single preference is observed for the 6-14 mm size of the *Acropora* genus (Temae: (Acr) 6-14 mm [0.015]). At Rotui, there is a preference for *Acropora* recruits smaller than 5 mm towards *L.sp3* (Rotui: (Acr) <5 mm [0.032]), as well as another preference for the "Other" genus (Rotui: (Oth) 6-14 mm [0.0219]). Coral recruits of the *Pocillopora* genus show positive outcomes for all three size classes.

For tnCCA, recruits of the larger size class (15-30 mm) at Temae show avoidances, while preferences are observed for recruits of the two smaller size classes for all three genera. Preferences for the *Pocillopora* and Other genera are slightly more pronounced for recruits smaller than 5 mm (Temae: (Poc) <5 mm [0.069]; (Oth) <5 mm [0.034]). Preferences for recruits smaller than 5 mm are also observed at Temae for these same genera, including the *Acropora* genus. Avoidances are noted for recruits larger than 5 mm for the *Acropora* genus.

The relationships of corals with the "OT" category, which includes bryozoans and sponges, showed mainly slightly positive results for recruits from the Rotui site, particularly with recruits of size class less than 5 mm. Only *Acropora* recruits showed slight positive results for sponges, except for the intermediate size class (6-14 mm) (Fig. 5).

The relationships of corals with the "OT" category, which includes bryozoans and sponges, showed mainly slightly positive results for recruits from the Rotui site, particularly with recruits of size class less than 5 mm. Only Acropora recruits showed slight positive results for sponges, except for the intermediate size class (6-14 mm) at Rotui (Fig. 5).

Corals

Strauss diagrams show that the 3 coral genera at the 2 sites show an avoidance of other coral genera, with very slight differences observed between coral sizes, but this remains minimal. This avoidance is slightly more marked at the Temae site, with avoidance rates higher than those at Rotui, and almost double in terms of negativity.

3.4. Interaction outcomes

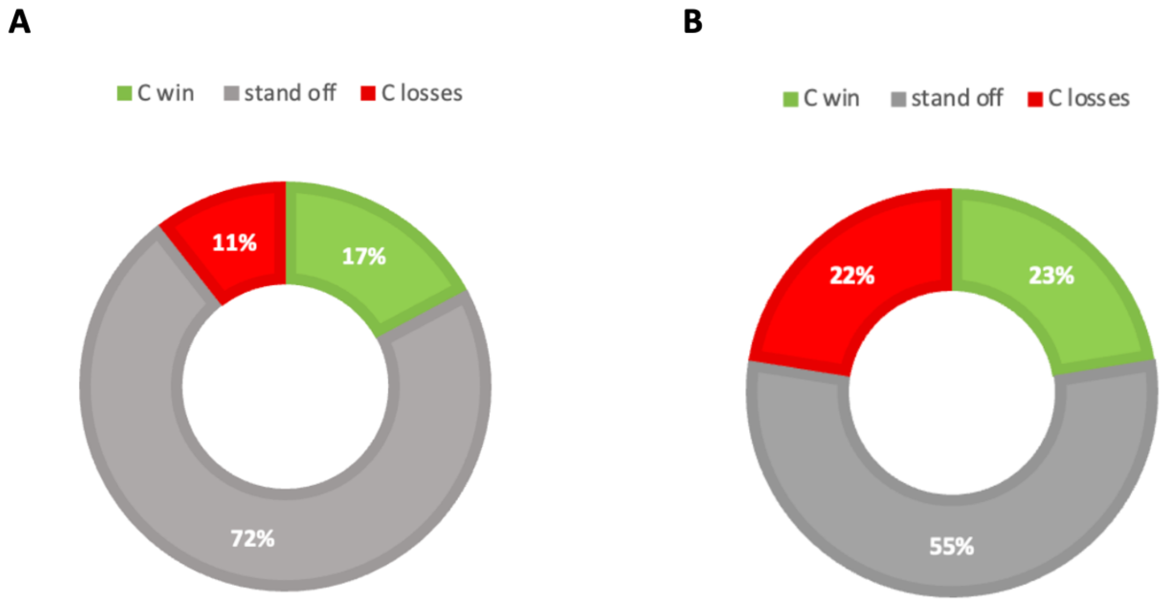


Figure 6. Competitive interaction outcomes between corals and 12 categories of organisms at the Temae (A) and Rotui (B) sites, classified according to the following 3 categories: coral win (green); standoff (grey); coral losses (red).

Taking all the categories of organisms together, the proportion of neutral interaction outcomes between individuals on this diagram was very high, especially at Temae (72%) (Fig. 6). At Temae, only 11% of negative interactions for corals and 17% of positive interactions were recorded out of a total of 256 interactions. At Rotui, neutral interactions represented around half of the total interactions (55%) with a higher proportion of negative interactions (22%) and slightly more positive interactions (23%) out of a total of 206 measurements.

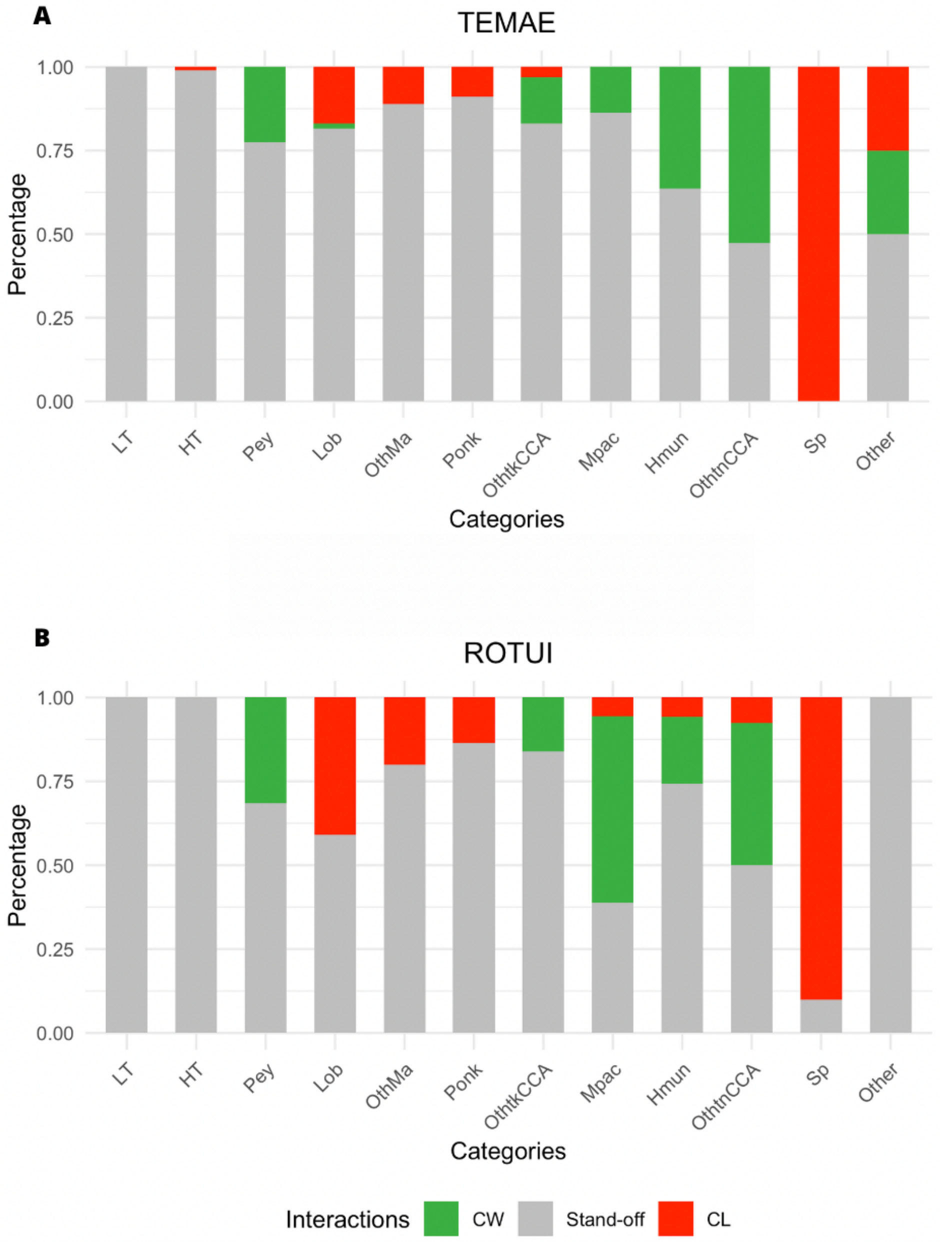


Figure 7. Detailed results of interactions between corals and the 12 categories of organisms on Temae (a) and Rotui (b) sites classified according to the 3 following categories: coral win (green); standoff (grey); coral losses (red).

Overall, both sites exhibited a relatively similar trend, however, for the majority of categories, the Rotui site recorded more negative interaction outcomes than the Temae site.

Firstly, turf algae displayed predominantly neutral interaction outcomes for coral recruits on both sites, with only 1% of interaction outcomes being negative for High Turf at the

Temae site. Within the 2 sites, the following macroalgae: *Lobophora* and the OthMa category (Other Macroalgae: *Turbinaria*, *Halimeda*, *Asparagopsis* and *Dictyota*) did not have any positive interaction outcomes with coral recruits, with respectively 40.8% and 20% negative interactions for Rotui and are slightly less negative for corals at Temae with 17% and 11% respectively and the remaining interaction outcomes being neutral. A very slight positive interaction with corals for *Lobophora* at Temae was recorded with 1.5%.

The results of interactions with *P. onkodes* were mainly neutral, with a number of negative outcomes for corals (9% at Temae and 13.6% at Rotui). The encrusting algae of the genus *Peyssonnelia* showed positive outcomes for corals at the 2 sites (22.5% at Temae and 31.6% at Rotui), the remaining were neutral. The majority of CCAs were found in small quantities, which is why they were grouped together in a category called Othtkcca comprising Other Porolithon (*Porolithon spp.), L. flavescens*, *M. pulchrum*, *D. conicum*, *N. megalocystum*, *H. sp.1* and thick CCA (*L. insipidium* only in Temae (quadrats)). At Rotui, this category showed positive (16.7%) and neutral interactions with corals, with no negative interactions recorded for Othtkcca at this site. All 3 types of interaction were recorded at Temae, of which 13.75% were positive and 3.12% negative.

Coral recruits had positive interaction outcomes with cryptic CCAs, namely *M. pacifica*, *H. minutum* and OthtnCCA. At Temae, coral recruits had a high percentage of positive outcomes with *H. mununitum* (36.4%) compared with 20% at Rotui. The latter site also exhibited 5.7% negative outcomes. On the other hand, corals studied at Rotui had a large percentage of positive outcomes with *M. pacifica*, compared with 13.8% at Temae. Again, at Rotui, a negative association for corals was present at 5.6%.

The latest categories, Sponges and Other (Bryozoans, Hc: Other corals and sand) showed negative interaction outcomes, particularly at Temae. At this site, all the coral-sponge interactions recorded had negative outcomes for corals, similar to Rotui with 90%. The Other category showed different results depending on the site, interacting 25% negatively and positively with corals at Temae and 100% neutrally with corals at Rotui.

4. Discussion

4.1. Reef Disturbances and Phase Changes Leading to the Current Reef State, Resulting in Alterations to Coral and Reef Organism Relationships`

A. Major reef disturbances: Heatwaves, cyclones, Taramea and overfishing

Heatwaves and Cyclones

Over the past few decades, French Polynesia has faced various types of disturbances, at both global and local scales, including several heatwaves that impacted the coral biodiversity of the islands. These heatwaves have had repercussions on coral mortality, fertility, and reproduction (Lamy et al., 2016; Speare et al., 2022), as well as on interactions between corals and organisms living within the reefs.

In total, seven heatwaves have been recorded, with three having major impacts on corals in 1991, 1994, 2003 (Salvat et al., 2008), as well as in 2019. This last year was marked by the largest heatwave recorded in over 30 years, resulting in the loss of more than 76% and 65% of corals from the Pocillopora and Acropora genera, respectively. This led to massive coral bleaching on the island of Moorea and affected the survival of microscopic coral recruits, reducing it by a factor of 10 (Speare et al., 2022). These disturbances have also had consequences on the data collected during this study, affecting coral coverage, coral recruitment, as well as the associations and interactions outcomes between reef organisms in Moorea.

Additionally, cyclonic disturbances related to the El Niño phenomenon also represent a major challenge for reef ecosystems(Smith et al., 2016). Several of these events have affected Moorea (Lamy et al., 2016), resulting in a decline in coral coverage on multiple occasions. These events can cause significant damage, leading to the substantial destruction of reef communities. It is important to note that Crustose Coralline Algae play a crucial role in the physical and structural maintenance of the reefs during such disturbances (Smith et al., 2016). However, it is worth mentioning that Moorea has not experienced devastating cyclones for several years, indicating that this disturbance did not influence the data collected for this study.

Acanthaster planci

Acanthaster planci (Fig. S5), commonly known as "Taramea" in Polynesian or crown-of-thorns starfish, are significant coral predators, contributing to the ecological disturbances observed in the reefs of Moorea over the past decades. These starfish have historically had significant impacts on reef ecosystems, particularly in terms of altering coral structure, as observed in the years 1978, 1982, and 2006 (Kayal et al., 2012).

It is worth noting that Taramea outbreaks, due to their low natural predation, have tended to proliferate within the reefs, leading to the degradation of coral populations (Kayal et al., 2012; Salvat et al., 2008).

In degraded coral environments characterized by reduced coral density, corals lose their dominant position. Consequently, Taramea have easier access to the preferred corals, facilitating their predation. However, in healthy coral sites with adequate coral density, it's possible to enhance coral survival by creating what could be described as "associative refuges." These refuges aim to protect corals by impeding predation by crown-of-thorns starfish, particularly *Acanthaster planci* (Kayal et al., 2011). The choice of corals by Taramea is governed by their dietary preferences, as seen in Moorea where corals of the Acropora genus are more severely affected during *Acanthaster* outbreaks (Kayal et al., 2011). This explains the results showing generally lower coral recruitment for Acropora corals on the two studied sites (Fig. 3). This can lead to a change in the dominant coral genus on the reefs (Lamy et al., 2016), with other genera dominating coral communities (Kayal et al., 2011).

When coral cover decreases due to *Acanthaster planci* outbreaks, there is a substantial reduction in herbivore density, particularly within fish communities (Lamy et al., 2016). These herbivores play a fundamental role in the development and life cycle of most corals. Even today, new outbreaks are occurring on the reefs of Polynesia, including Moorea, and starfish population surveys are ongoing at CRIOBE.

Overfishing and Human activities

Overfishing is one of the causes of coral community degradation and a driving factor in their decline (Smith et al., 2010). It affects a large portion of organisms in reef ecosystems, such as herbivorous fish and coralline crustose algae, resulting in reduced coral cover (Pandolfi, 2003; Salvat et al., 2008; O'Leary et al., 2012; Smith et al., 2016). Human activities such as overfishing promote the proliferation of coral competitors, especially macroalgae (Smith et al., 2010, 2016) leading to increased competition with corals. This competition influences and determines the structure and abundance of organisms on the reefs, consequently impacting relationships and interactions among these organisms (Hughes, 1995; McCook, 2002; Titlyanov et al., 2007). All of these disturbances, including those detailed in the subsequent conclusion, exert a substantial influence on the structure of reef ecosystems, resulting in significant impacts on aspects such as reproduction, mortality, diversity of coral species, and interactions among the organisms in Moorea's reefs.

B. Phase Shift: Transition from Coral Dominance to Macroalgal Dominance in Reefs

The phenomenon of "phase shift" is observed and described on some reefs worldwide (Hughes, 1995; McCook et al., 2001; McManus and Polsenberg, 2004; Barott et al., 2012; Smith et al., 2016; Bittick et al., 2019; Vieira, 2020). This shift occurs when the proportion of hard corals (Scleractinians) decreases, giving way to a rapid proliferation of macroalgae (McManus and Polsenberg, 2004). Environmental disturbances such as those detailed previously can be the cause of this phenomenon (McCook et al., 2001), including heatwaves, *Acanthaster* outbreaks, and overfishing. As a result, corals lose their dominant position on the reefs. Under these conditions, several genera of macroalgae are known to be invasive. As mentioned earlier, algae like *Turbinaria* (Bittick et al., 2019), *Lobophora*, and turf algae are described as "opportunistic" algae taking advantage of the reduced coral cover to proliferate (Salvat et al., 2008; Smith et al., 2016; Vieira, 2020).

As illustrated in this study, these algae are present in significant quantities in the results of the benthic cover analysis at the two study sites (Fig. 4). The actions of these algae could accelerate reef degradation while influencing the relationships between ecosystem organisms. However, there is no significant evidence of a shift to a phase dominated by macroalgae within the two sites, even though there has been a recent proliferation of algae in Polynesia (Theophilus et al., 2020). Nevertheless, the impacts of cumulative disturbances lead to the reduction of reef-building corals, which could potentially lead to a new reef state with a predominance of algae (McManus and Polsenberg, 2004). Reefs that undergo 'phase changes' with a reduction in their coral (Kuffner et al., 2006) lead to a greater number of interactions of a negative nature for recruits caused by the more abundant presence of certain organisms at Rotui. Considering the results obtained, which reveal lower coral recruitment at the Rotui site (Fig. 3) and a greater abundance of macroalgae at this site (Fig. 4), it is possible to envisage a potential trend towards a phase change, although this currently remains hypothetical. Additionally, anthropogenic activities directly contribute to the decrease in coral cover, providing space for direct coral competitors like macroalgae (Smith et al., 2016)

Reef health can be measured by quantifying coral cover. Healthy reefs have ideal coral cover, generally between 50% and 60% (Done, 1982; Connell et al., 1997; Salvat et al., 2008). In contrast, reefs that have undergone major deteriorations, such as bleaching or *Acanthaster planci* infestations, often display coral cover below 10% (critical threshold) (Salvat et al., 2008). Evaluating a reef's health status can also be done using other types of benthic organisms to achieve optimal precision, closer to the reality (Smith et al., 2016).

In conclusion, disturbances affect not only corals but also macroalgae. The recolonization of fleshy macroalgae in a degraded reef environment does not necessarily occur immediately after a disturbance (Cheal et al., 2010; Schmitt et al., 2022). However, in the presence of low herbivory or when herbivory is weakened, the time required for macroalgae recolonization can be significantly accelerated. Furthermore, some disturbances have a more pronounced impact on corals, especially heatwaves, which affect corals more due to their lower thermal resistance compared to macroalgae like *Turbinaria* (Stiger and Payri, 1999; Anton et al., 2020). This inevitably hinders coral recruitment as larvae struggle to settle in their environment (Kuffner et al., 2006; Smith et al., 2016).

It is important to note that corals can regain significant coverage rates over varying periods, which can be rapid, less than five years in certain cases (Diaz-Pulido, 2009) or take several decades (Van Woesik et al., 2011; Schmitt et al., 2022). This is why herbivore grazing is essential, as it mitigates competition between organisms like corals and coralline algae with macroalgae by reducing macroalgal abundance. This helps maintain optimal relationships between these organisms, preserving the reef's coralline algae species and the survival and growth of corals (Mumby and Harborne, 2010; Mcleod et al., 2019).

4.2. Difference in coral health and recruitment between Rotui and Temae reefs

The study sites at Rotui and Temae are both located on the outer slope of Moorea Island but differ in their management. The Temae site is situated on the edge of the Nuarei Marine Protected Area (MPA) (Salvat et al., 2008), enjoying the benefits of this protection, including a greater abundance of herbivorous organisms (Mumby and Harborne, 2010). Herbivory plays an essential role in reef ecosystems, as herbivorous fish populations have the ability to control macroalgae through grazing, thus reducing competition between corals and macroalgae by

limiting their presence. The significant presence of herbivorous fish also enhances coral recovery rates (Mumby and Harborne, 2010).
In contrast, the Rotui site is subject to fishing regulations but does not have MPA status, resulting in a lower abundance of herbivorous organisms. Some studies have shown that low or reduced herbivorous fish populations can have a negative impact on coral abundance (McCook et al., 2001; Rasher and Hay, 2010) by favoring the rapid growth of fleshy algae commonly found on reefs (McCook, 1999; Smith et al., 2010, 2016).

At Temae, where direct and indirect competition with macroalgae appears to be lower and herbivore presence is more significant, crustose coralline algae (CCA) and corals thrive more (Smith et al., 2010). CCA play a fundamental role in the reef ecosystem (Smith et al., 2016). A protected site, such as Nuarei on the edge of Temae, tends towards greater diversity and abundance of CCAs (O'Leary et al., 2012), especially when macroalgae presence is low. This also promotes coral recruitment, as shown in Figure 3b, where Temae has lower macroalgae levels (18.3%) compared to Rotui (30.1%), along with a higher abundance of CCA and coral recruitment (7.78 versus 5.61 recruits/m^2).

The study site at Rotui serves as an example of a location with moderate health, characterized by a relatively low average coral cover of 11.5%, approaching the critical threshold of 10% (Fig. 4) (Salvat et al., 2008). In contrast, the Temae site exhibits an average coral cover of approximately 24%, indicating better health. This difference is also reflected in the rates of macroalgal cover, suggesting that the two sites may be in slightly different 'phases' in the future.

Reef sites worldwide (Smith et al., 2016; Hughes et al., 2018; Mcleod et al., 2019), including those in the Caribbean (Gardner et al., 2003), the Great Barrier Reef (De'ath et al., 2012) and Pacific reefs (Bruno and Selig, 2007), have also experienced significant losses in coral cover (Smith et al., 2016). Consequently, the significant presence of macroalgae results in reduced space for the development of crustose coralline algae (CCA) and corals, leading to increased competition at Rotui, where they are more developed, resulting in different patterns of coral-coraline association and interactions. This is shown by the high frequency of negative outcomes with coral recruits at this site, notably for the smallest recruits (Fig. 5), as well as the negative interactions outcome recorded in Figure 7. The Temae site generally recorded more neutral interaction outcome and around half as many negative interaction outcomes as Rotui, indicating potentially weaker competition (Fig. 7).

Furthermore, it is important to note that the imbalances observed between the sites are not necessarily attributable to a single factor. As mentioned earlier, crown-of-thorns starfish (Taramea) play a significant role in reducing coral cover and impacting herbivore populations (Lamy et al., 2016) but that's not the only disturbance. However, it is essential to recognize that the impact of Taramea can vary considerably from one site to another, resulting in reduced coral cover and, consequently, decreased coral recruitment in the most affected areas. It should also be noted that trophic fish groups are likely to experience a significant decline when coral cover is around 10%, especially if it drops below this figure, due to an outbreak of *Acanthaster planci* (Lamy et al., 2016), or following a coral bleaching event (Salvat et al., 2008). Given that the coral cover at Rotui is very close to this critical threshold, it is conceivable that *Acanthaster* is having an impact on the observed low rate. However, as mentioned above, in the context of this study it is likely that multiple disturbances contribute to this phenomenon.

One plausible hypothesis is that Rotui has been and remains more exposed to these stressors than the Temae site. This situation could partly explain the low coral cover observed, as well as the reduced levels of crustose coralline algae (CCA) cover (O'Leary et al., 2012). To conclude, it is evident that the two sites are differently affected by the disturbances experienced on Moorea Island, resulting in varying interactions among organisms between the Rotui and Temae sites.

4.3. Interactions and outcomes between Corals-CCA and Corals-Macroalgae

A. Coral – Non-Cryptic CCA

P. onkodes

As for the GBR reefs (Harrington, 2004), it is the CCA species *P.onkodes* that stands out for its predominant presence on the two coral reefs in the study, displaying a ratio five times higher on the Temae reef, where its coverage reaches approximately 15.2%. This percentage is equivalent to more than half of the total coverage of these calcified coralline algae at the Temae site, which is 26.8%. The results reveal some differences in the preferences and avoidances of the three categories of coralline genus, namely Acropora, Pocillopora and other genera, according to their size in relation to this CCA. In particular, the smallest recruits (less than 5 mm), especially those from the Acropora genus, showed a more pronounced avoidance of this CCA species compared with all the other non-cryptic CCAs, especially at the Temae site, which could be attributable to the increased abundance of this CCA at this location. In addition, this CCA develops in exposed environments, where the activity of grazers is more intense, making this habitat potentially dangerous for coral recruits and thus explaining their avoidance behaviour (Fig. 5). Specifically, CCA *P.onkodes*, as an exposed species on reefs, progressively surrounds coral recruits as they grow. This dynamic stems from the increasing need for light and space to allow recruits to achieve optimal growth, inevitably leading to an increase in their exposure. As a result, larger coral recruits are more likely to interact with organisms that prefer exposed habitats. This observation explains the positive results observed in recruits from the larger size class (15-30 mm) with *P.onkodes*.

On the other hand, the percentage of negative interactions recorded was 13.6% for the Rotui site and 9% for Temae. The remainder were mainly neutral interactions with recruits, with no positive associations observed between these organisms on either reef (Fig. 7). It is likely that the lower coverage of *P. onkodes* at the Rotui site is due to more intense competition with the predominant benthic organisms. Furthermore, the finding that negative interactions on corals are more frequent at Rotui, despite the lower quantity of *P. onkodes* compared with the Temae site, confirms that this CCA may be influenced by the environment and, consequently, interact more negatively with coral recruits.

The CCAs are predominantly neutral or benevolent competitors in their relationships with corals, which aligns with existing literature (Barott et al., 2012; Smith et al., 2016) and this study confirms this trend. However, some studies have indicated that *P. onkodes* may have adverse effects on corals, as observed in the North Pacific, where it has been demonstrated that *P. onkodes* is associated with certain coral diseases due to their Operational Taxonomic Units (OTUs) favoring these diseases, in comparison to other coralline species favoring antimicrobial compounds such as *H. reinboldii* (Quinlan et al., 2019). The quantity of CCA present on reefs depends on the intensity of competition among organisms, particularly with macroalgae (O'Leary et al., 2012). For this reason, the coverage of CCAs relies on the rate of herbivores, such as fish, which will limit these potentially invasive competitors. It is also noteworthy that all recorded negative interactions with this CCA were direct, occurring through the overgrowth of coral recruits.

In addition, some CCAs use a highly effective anti-fouling mechanism consisting of the exfoliation of epithelial cells to prevent coral larvae from settling on their surface, as observed in several CCAs, including *P. onkodes* (Harrington, 2004). This process could be one of the explanations why this CCA does not establish positive associations with coral recruits.

The fact that the same coralline species, such as *P. onkodes*, is found in different places on Earth could be linked to the diverse microbiomes present on their surfaces, which might be incompatible with certain coral genera or species. It is more likely that certain molecules associated with CCA cell walls that can also induce the settlement of recruits (Tebben et al., 2015; Quinlan et al., 2019) are different and not recognised by the latter.

Another way in which coral larvae recognise CCAs is by identifying the bacteria that cover them (Tebben et al., 2011; Sneed et al., 2014; Quinlan et al., 2019). In addition, larvae show preferences for settling on certain CCA species (Harrington, 2004; Quinlan et al., 2019). It is conceivable that the coral larvae of the species present in Polynesia react differently to the bacterial signals present on the surface of *P. onkodes.* Indeed, each CCA species harbours specific bacterial communities, which vary from one species to another (Barott et al., 2012; Sneed et al., 2015). Furthermore, it is likely that a distinct environment can alter these bacterial communities, resulting in different associations and interactions. It is also conceivable that other coral genera, apart from those specifically studied here, could be attracted to this coralline. However, surveys carried out for corals in the 'other' genus category, which includes genera other than Acropora and Pocillopora, did not show this result.

However, it is important to note that environmental conditions are likely to play a major role in these interactions. It is plausible to speculate that if the Rotui and Temae sites were characterised by more substantial coral cover, perhaps reaching the optimal level of around 50-60% (Done, 1982; Connell et al., 1997; Salvat et al., 2008), the interactions between recruits and the CCA *P.onkodes* might be different. In such environments, it is likely that interactions between recruits and this coralline would be less unfavourable, as coral dominance on the reef would reduce competition between organisms, particularly with macroalgae. It is therefore conceivable that coral recruits could establish less negative interactions with this CCA in sites where reef health is more robust. Consequently, collecting data on this coralline in healthier environments could prove instructive for a more in-depth understanding of these interactions.

Other exposed CCAs

The Othtkcca category, encompassing all non-cryptic CCA studied except for *P.onkodes*, predominantly exhibited neutral interactions with coral recruits (Fig. 7). This classification was chosen due to a limited dataset for these CCA species, aiming to ensure more relevant results. The results also revealed some positive associations between certain CCAs in this category and coral recruits (Fig. 7), although their frequency was low. This includes species like *L. insipidium* on Temae, previously associated in the literature with inducing metamorphosis in certain coral recruit species (Heyward and Negri, 1999). Other species within the genus Porolithon, *D. conicum*, and *M. puluchrum* also contributed to the positive aspect of the OthtkCCA category, with the latter two exclusively found on Rotui (Fig. 7). However, it is evident that these positive results do not fully capture the entirety of interactions between these CCAs and coral recruits. A more comprehensive data collection could unveil interactions of diverse nature. For instance, according to the literature, *D. conicum*, corresponding to the CCA *Pneophyllum conicum* (Dawson), seems to have relatively negative interactions with corals (Keats et al., 1997). The observed negative part on the Temae site for this category corresponds to *L. insipidium,* also recorded negatively. It is clear that the quantity of positive and negative interactions recorded for the recruits does not fully reflect natural association patterns.

The results from the Strauss model revealed that the majority of coral recruits tend to avoid exposed CCA, primarily indicated by negative outcomes (Fig. 5). This trend can be explained by considering that recruits avoid exposed environments where these CCA flourish, due to various factors such as predation by different organisms, herbivore grazing, and competition with other benthic organisms like macroalgae (Doropoulos et al., 2016; Smith et al., 2016). This explanation could account for the more systematic avoidance of exposed species compared to cryptic species, especially for smaller recruits (Fig. 5).

It is crucial to note that the majority of CCA species studied generally showed neutral interactions with corals in this study (Fig. 7), a finding consistent with existing literature (Barott et al., 2012; Smith et al., 2016). The records of CCA collected in this study reveal that CCA, including *L. flavescens, N. megalocystum, H.sp.1*, as well as thick CCA, consistently displayed entirely neutral interactions with corals on both reefs studied.

It is also conceivable that with data collection conducted in healthier reef sites characterized by more abundant populations of CCA and corals, a more substantial sampling (in terms of interaction observations) of associations between these less common CCA and coral recruits could be obtained. Such an approach could reveal interactions different from those identified in our current study, applicable to all organisms recorded in very low quantities that do not allow for a general trend close to reality.

B. Coral - Cryptic CCA

Furthermore, positive interactions between coral recruits and cryptic CCA are substantial, displaying high percentages of association, particularly notable at the Temae site where fine CCA represent over 50% of positive associations. This means that one out of two recruits in contact with this CCA establishes a positive association, a similar trend being observed for *M. pacifica* on Rotui (Fig. 7). It is established that coral settlement is more significant in cryptic habitats than in exposed habitats (Doropoulos et al., 2016). The highly positive associations observed support the previously formulated hypothesis and also demonstrate that recruits are significantly more associated with cryptic CCA. This correlation is logically explained by the fact that recruits primarily settle in sheltered, relatively cryptic locations offering the most favorable conditions for their survival and development. Cryptic CCA thrive in similar environments, explaining a higher quantity of positive associations for coral recruits (Fig. 7).

Moreover, the results reveal that coral recruits at the Rotui site are the only ones to show a percentage of negative interactions, albeit slight, with cryptic algae *H. munitum, M. pacifica,* and *L. sp.3*, predominantly displaying neutral and highly positive associations with coral recruits from both sites (Fig. 7). This observation may be linked to the health status of the site, where competition is more intense at Rotui. The increased presence of macroalgae on this site could result in a more restricted space for the development of these CCA. This competitive pressure for space could explain why these CCA grow on coral recruits, seeking to cope with this constraint.

Furthermore, the observations on interactions between coral recruits and cryptic CCA (Fig. 7) seem consistent with the results revealed in the Strauss model (Fig. 5). Overall, *H. munitum, M. pacifica*, and fine CCA showed significantly more positive outcomes for coral recruits than exposed CCA on both study sites. In general, *H. munitum* shows a positive outcome for all coral recruits in the smallest size class (5 mm) and all recruits regardless of their size on Rotui. Although slightly less positive, *M. pacifica* shows much more positive results than all exposed corallines. The general trend indicates that smaller-sized recruits (5 mm) show more strongly positive results for fine CCA, especially on the Rotui site. A similar trend can be observed at the Temae site, although slightly less pronounced (Fig. 5). These positive outcomes can be explained by the fact that recruits, by preferentially choosing sheltered (cryptic) habitats, seek to avoid potential threats to their survival and development. At Rotui, the increased presence of macroalgae could further encourage recruits to develop in cryptic habitats, where light is less abundant, resulting in less prosperous macroalgae growth.

Finally, it is important to stress that competition between corals and CCAs does not appear to be detrimental to corals (Barott et al., 2012).

C. Coral - Macroalgae

Peyssonnelia

The red macroalgae belonging to the *Peyssonnelia* genus are not found in high abundance on the two examined reefs (Fig. 4). However, their interactions with corals were mainly recorded as neutral, and positive for coral recruits (Fig. 7). On several occasions, we have observed this macroalgae associated with various coral species listed in the database, particularly the genera Acropora and Pocillopora (Fig. S8), This macroalgae exhibits positive outcomes with corals belonging to three different size classes and within all three categories of coral genera (Fig. 5). It appears that the interaction of this algae with corals is beneficial as it acts as a substrate facilitating their colonization. All sizes of recruits show positive outcomes in their relationships with this macroalgae, especially small-sized recruits. Furthermore, various studies have demonstrated the crucial role of algae of the *Peyssonnelia* genus in attracting coral larvae and promoting their metamorphosis (Morse et al., 1996; Heyward and Negri, 1999; Harrington, 2004). In addition, these positive results can be explained by the fact that this alga was mainly cryptic in this study, also explaining its positive outcomes with the smallest recruits (5 mm) for the majority of coral genera, such as the genus *Acropora* on the 2 study sites (Fig. 5).

However, it is important to note that the scientific literature presents varied results regarding the role of *Peyssonnelia* in the metamorphosis of coral larvae. For example, several studies conducted in the Caribbean have shown that certain species of *Peyssonnelia*, such as *Peyssonnelia sp*. (a single species but not specified) and *Peyssonnelia spp.* (referring to several species), do not seem to attract or interact with coral larvae (Antonius, 1999; Houk and Musburger, 2013; Ritson-Williams et al., 2014). One plausible hypothesis is that this phenomenon could be associated with the various species of *Peyssonnelia*, which have varying levels of inductive power. These results differ from those of the present study and of certain studies carried out in Australia, where it is also presented as an alga that helps larvae settle and induces metamorphosis (Heyward and Negri, 1999; Harrington, 2004; Quinlan et al., 2019).

Our study reveals that corals of all sizes and various genera, including Acropora and Pocillopora, show a clear preference for the *Peyssonnelia* algae, regardless of the site (see Fig. 5). *Peyssonnelia* has the most positive impact on corals of small sizes, below 15 mm, reinforcing the idea that it seems to be particularly positive and beneficial for coral recruits during their early growth stages, including larval settlement, metamorphosis, and initial growth.

Metamorphosis induction by *Peyssonnelia sp.* has been observed in several coral species, particularly in the Pacific, but also in the Caribbean (Morse et al., 1996; Harrington, 2004). Moreover, given that the coral settlement and metamorphosis process is more favorable in the presence of this algae, it is reasonable to observe positive interactions between corals and the algae. These explanations could contribute to understanding the high rate of positive interactions observed in Figure 7. It is interesting to note that the quantity of *Peyssonnelia* is almost twice as high on the Rotui site (3.4%), suggesting more intense herbivory on the Temae site. *Peyssonnelia*, like other non-calcifying macroalgae, is likely preyed upon by herbivores. This could suggest that is due to *Peyssonnelia* being more preyed upon by consumers.

Lobophora

The presence of *Lobophora* on the reefs is significantly higher at Rotui, reaching 20.2%, compared with the site studied at Temae, where it represents 9.6% of the cover (Fig. 4). In light of the previous observations, the abundance of this alga appears to be influenced by the management of the Rotui site, unlike the situation at Temae, located on the outskirts of the marine protected area. This suggests that the quantity of macroalgae is linked to the potentially reduced presence of herbivores at the Rotui site

The results suggest that interactions between corals and *Lobophora* are primarily unfavorable, with particularly high levels of negativity observed in the corals at Rotui, reaching a total of 40.8% negative interactions. This high proportion of negative interactions outcome is directly related to the significant abundance of this algae at the Rotui site, and it is also the most widespread non-calcifying macroalgae on Moorea Island (Mumby et al., 2016). Consequently, this alga stands out as the main source of negative interactions with corals, being a genus of macroalgae that maintains significant interactions with corals (Jompa and McCook, 2002; Nugues and Bak, 2006; Mumby et al., 2016), as well as with other organisms. Records of interactions between *Lobophora* and corals have mainly revealed that these algae tend to cover young corals (Fig. S9) explaining the majority of negative interactions observed for corals in the results (Fig. 7). This ability of *Lobophora* to overgrow corals gives it a significant advantage in competition with other sessile organisms, as it blocks the light needed by corals (Barnes D., 1990; McCook et al., 2001; Titlyanov et al., 2007; Smith et al., 2016).

These algae play a crucial role in the competition for space on the reef, as they are highly opportunistic organisms with potentially excessive or invasive growth, especially in degraded sites or those with low coral cover (Vieira, 2020). This so-called "indirect" competition (Titlyanov et al., 2007) affects most reef organisms, leading to a reduction in coral recruitment, as previously detailed. The *Lobophora* genus of algae is recognized as a potent inhibitor of coral recruitment (Evensen et al., 2019).

In some cases, the overgrowth by certain *Lobophora* species can induce coral bleaching upon contact, as observed in a previous study in the Caribbean (McCook et al., 2001). It is possible that certain *Lobophora* species in Polynesia maintain similar interactions.

It is worth noting that some species of *Lobophora* show varying degrees of opportunism, and not all are equally opportunistic. Only certain *Lobophora* species take advantage of degraded reefs to develop significantly (Vieira, 2020). In the presence of normal reef conditions, characterized by an adequate proportion of coral cover, these algae can coexist with corals without causing negative interactions for the latter (Vieira, 2020). Furthermore, shading created by certain algae such as *Lobophora*, as well as *Turbinaria*, can sometimes be beneficial for corals by protecting them from damage caused by bleaching (Jompa and McCook, 1998; Titlyanov et al., 2007).

Other Macroalga

Similar to *Lobophora*, the structure of *Turbinaria* has the potential to block light essential for corals, particularly impacting smaller coral recruits with limited surface area for light capture (McCook et al., 2001; River and Edmunds, 2001; Titlyanov et al., 2007). Turbinaria algae, however, does not exhibit allelopathic effects as potent as *Asparagopsis* and *Dictyota* (Longo, 2016). In this study, *Turbinaria* has shown neutral interactions with recorded recruits, potentially due to limited contact with this macroalgae.

While both Rotui and Temae sites exhibit similar *Dictyota* algae coverage, Rotui records more negative interactions, particularly with the OthMa category, which includes *Dictyota*. Negative interactions are prevalent in the OthMa category, mainly caused by *Dictyota* and other unidentified macroalgae. Coral recruits strongly avoid the OthMa category, influenced by *Dictyota* and other unidentified macroalgae, leading to more negative interactions at both sites. The impact of *Dictyota* on corals, such as larval settlement and growth, are more severe than those of *Lobophora* (Diaz-Pulido, 2009; Foster et al., 2008; Box and Mumby, 2007). *Dictyota* can negatively affect corals through secondary metabolites, leading to reduced photosynthetic efficiency and, in some cases, coral mortality.

Compared to *Dictyota*, *Asparagopsis* is more abundant on Rotui, absent on Temae (Fig. 4), potentially colonizing degraded environments during coral bleaching (Diaz-Pulido; McCook 2002). Although no negative interactions were recorded with corals on Rotui, the limited contact with corals makes these results inconclusive (Fig. 5 and Fig. 7). *Asparagopsis* also produces liposoluble compounds with allelopathic effects similar to *Dictyota*, especially with the species *Asparagopsis taxiformis*, which is abundant in French Polynesia (Longo and Hay, 2017). *Asparagopsis taxiformis* is highly ubiquitous and can be found in different oceans worldwide (Greff et al., 2017). In the Mediterranean, this alga produces bioactive compounds (secondary metabolites) on its surface when interacting with coral, inevitably affecting corals (Greff et al., 2017). The impact of this alga is significant and can even extend to herbivores, such as the fish *Acanthurus triostegus*, which uses chemical signals to reduce grazing pressure on the reefs (Gache et al., 2019), providing protection and promoting increased growth, leading to the proliferation of this alga. This expansion inevitably results in an increase in negative interactions with corals, potentially compromising their survival. Indirectly, this situation intensifies competition among organisms on the reefs, potentially impacting coral recruitment rates.

Turf algae

The results mainly revealed neutral interaction between these recruits and the turf algae (Fig. 5). As the coral recruits studied had recently settled on the substrate, such as on the CCAs, one hypothesis could be that these coral recruits benefit from a 'protection' offered by their association with these CCAs, increasing their chances of survival, in particular by avoiding being invaded by turf algae (Harrington, 2004). Moreover, some of the numerous neutral interactions observed may stem from the corals' energetic investment aimed at mitigating the potential negative effects of these interactions (Barott et al., 2012). It is crucial to emphasize that this dynamic is particularly relevant for the youngest recruits, which have not yet reached reproductive maturity and thus have a greater amount of energy for their defense (Babcock, 1991; Soong and Lang, 1992; Soong, 1993; Barott et al., 2012). This observation is applicable across all studied macroalgae.

However, it is important to note a difference between low turf and high turf algae. Low Turf algae are predominant at Rotui, leading to strong avoidance reactions in recruits and young corals of all genera. At Temae, on the other hand, the proportion of Low Turf is much lower, and this did not provoke avoidance reactions in coral recruits, except for the genus Acropora (Fig. 5.B). No avoidance interactions were observed when all genera were combined (Fig. S11). In addition, analysis with SIMPER showed that Lowturf accounted for a significant proportion of the dissimilarities between the two sites (Tab. 1), with a presence 2 times greater at the Temae site (Fig. 4). These observations underline the importance of considering the quantity of turf algae present, which can vary according to the characteristics of the sites studied. This provides a better understanding of the interactions between developing corals and turf algae. This provides a better understanding of the interactions between developing corals and turf algae.

On the Rotui site, where coral cover is reduced due to coral decline or weakening (bleaching, diseases, disturbances), an ideal "bare" substrate is created for the development of turf algae (Titlyanov et al., 2007). Like *Lobophora*, these algae are characterized by very rapid growth, and turf algae are among the first macroalgae to colonize "open" spaces (Smith et al., 2016). This trend explains the high number of individuals recorded in this study, where the total cover of turf algae (LowT and HighT) represents nearly half of the total coverage in Rotui and about 30% in Temae (Fig. 4). The proportion of LowTurf reaches 33% of benthic cover on the Rotui site, compared to 16% on the Temae site (Fig. 4), possibly related to the potential rapid colonization of newly opened spaces on the Rotui site.

Benthic turf algae have the ability to disturb benthic organisms, depending on their size, by growing on them. This applies especially to scleractinian corals and fleshy macroalgae, particularly when space is limited (Ritson-Williams et al., 2005; Puyana and Prato, 2013; Bakker et al., 2016, 2017; Ford et al., 2018). Additionally, in certain situations, the presence of these algae can hinder the settlement of coral larvae on their substrate due to microbial activity (Connell et al., 1997; Smith et al., 2016). Furthermore, the abundant presence of turf algae reduces the available space on the seabed, limiting the available surface area suitable for the development of reef organisms (Arnold and Steneck, 2011; Smith et al., 2016; Vermeij and Sandin, 2008). This situation creates competition, especially for space, the intensity of which varies depending on the organisms and can be detrimental to corals (McCook et al., 2001; Rasher and Hay, 2010; Barott et al., 2012; Smith et al., 2016). This competition is also influenced by the site's health (Barott et al., 2012). Additionally, turf algae have a strong negative influence on larval survival, as indicated by the results showing that smaller coral recruits exhibit a greater tendency to avoid them compared to those in other size ranges, regardless of their genus (Fig. 5).

In general, it is observed that macroalgae are not beneficial for coral recruits, even as they develop into more mature corals, consistent with the expected outcomes (Arnold and Steneck, 2011).

D. Coral - Other categories

Sponges

According to field observations, a species of red sponge was very attracted to the recruits studied, although the percentage of benthic sponge cover was relatively low on the 2 reefs studied (Fig. 4). Despite their rarity, the results of their interactions with coral recruits were very negative (Fig. 7). This trend is less obvious in Fig. 5 because sponges were grouped together in the OT category due to their low abundance. The OT category includes both sponges and bryozoans, with a predominance of the latter, which attenuate the avoidance responses of sponges, leading to less negative results. Given the low number of individuals, it seems unlikely that competitive pressure can explain the very harmful interactions of these organisms on corals. In most of the world's reefs, sponges are essential organisms, particularly for improving water quality, and have beneficial aspects for corals. However, they are frequently associated with damage to corals (Pawlik et al., 2007).

Coral - corals

Corals have shown strong avoidance behavior towards other corals, especially at Temae, where the rates of avoidance between different corals are high (Fig. 7). This may reflect a site with a higher coral cover compared to Rotui, which inevitably leads to more interactions with other corals on the site. This can also be observed in the figure 7 where some negative interactions are recorded between corals themselves at Temae (Fig. 7). Furthermore, these interactions have highlighted that interactions between coral recruits and other coral recruits (or even corals) can sometimes be positive for some recruits that were covering other corals.

4.4. General discussion

A. Potential optimization of the methods used for the study of associations and interactions.

Selection of several sites

It would be relevant to explore associations and interactions across multiple sites in Moorea, each subjected to different management regimes, to determine if significant differences can be observed within the same island. Comparing two marine protected areas (MPAs) like Motu and another MPA, known for their high abundance of herbivores, corals, and CCA, with two sites under regulated fishing, such as Rotui, and two unprotected sites farther from MPAs, could provide valuable insights. A more accurate representation of recruitment rates and patterns of interactions and associations with corals, with a considerable degree of precision, could be established.

Furthermore, the study of two sites Rotui and Temae displaying different health states has already revealed variations in interactions among organisms, influenced by contrasting environmental conditions. It would be necessary to sample a minimum of 500 coral recruits for each site to generate a significant volume of data, ensuring a realistic representation of associations between corals and CCA, as well as interactions between corals and non-calcified macroalgae. Conducting a second sampling (replicate) at a highly healthy site, characterized by elevated CCA and coral abundance, could potentially increase the quantity of CCA, providing additional insights into species that appear to benefit corals such as *M. pacifica*, *L. sp.3* and *H. munitum* (Fig. 5), some of which are rarer. This approach would yield more realistic and distinct patterns in associations and interactions between coral recruits and CCA.

It's important to note that due to the limited data available for some organisms, even slight variations, such as a few additional individuals, can lead to significant changes in the percentage of interactions, as observed for certain non-cryptic CCA, but also for the sponges and HC (Corals) categories (Fig. 7). Furthermore, the rarity of these organisms in contact with coral recruits suggests their infrequent occurrence in the reef habitats where recordings were made, as observed in Rotui (Fig. 4), where coral coverage is lower. Consequently, there are fewer opportunities for contact between coral recruits and these organisms, emphasizing the influence of the environment on interactions between recruits and other benthic organisms, while also reflecting the nature of this habitat.

Choice of size

In order to avoid any intrusiveness related to sample collection for complex identifications and to facilitate the identification of coralline species specific to French Polynesia, which are currently insufficiently documented, a sensible approach would be to use equipment that offers increased precision. This would help optimize the expertise required for CCA identification (Quinlan et al., 2019).

Reef ecosystems are characterized by their dynamism, with conditions that can change rapidly. Corals, from their larval settlement to a size of 30 mm, evolve in different environments and on different substrates. Indeed, recruits that have reached this size have already established their presence on the benthos for some time.

Therefore, it would be appropriate to prioritize slightly smaller coral recruits than those reaching 30 mm. In general, this size corresponds to an age of approximately 2 years for corals under favorable conditions. Additionally, it's worth noting that in a disturbed environment like Rotui, where conditions are not conducive to the growth of recruits and corals, it is possible that the recruits are older than those in a healthy site where corals have been able to grow favorably to reach the same size. This variability should be considered, as in such cases, associations between corals and CCA may no longer be visible due to their age.

In addition, broadening the range of coral genera that can be readily identified at the study site could significantly improve the accuracy of the association analysis. This would allow us to identify several distinct patterns of association between different coral genera and different CCA species. This diversity of information would be essential for an in-depth understanding of the complex ecological dynamics within these coral ecosystems.

B. Discussion about the study Analysis Method and Parameters

Strauss Linear Selection Index

Strauss' linear selection index, a commonly used tool in population ecology (Strauss 1979; Mantyka, 2007; Madduppa, 2014), was adapted to our study to analyse coral preferences and avoidance of organisms in direct contact with them. This approach has also been used to quantify the food preferences of marine species of herbivores (Mantyka and Bellwood, 2007; Madduppa et al., 2014). Applying this index allowed us to quantify coral preferences and avoidance, assessing their intensity for each of 20 distinct categories of organisms. This analysis is crucial for understanding the interactions/relationships between organisms, a determining factor in the dynamics of coral reefs. It's essential to note that only one replicate per site was established, making it impossible to conduct statistical analysis. Therefore, this index should be interpreted as indicative.

A larger dataset would have been more favorable to gain a more accurate insight into coral preferences and their avoidance of CCAs. Due to the limited data available on CCAs and the ambiguous relationships between corals and CCAs, some categories produced results that do not faithfully reflect the reef's dynamics, especially concerning non-cryptic CCAs like *N.megalocystum, M.pulchrum, Lflavecens, H.sp1*. While the field records did not indicate negativity for some organisms with corals recruits, Strauss' linear selection index highlights that corals tend to avoid specific sizes and genres within these categories. Despite these limitations linked to the fact that a single replication was carried out, the index offers insights into the preferences of corals and their avoidance of surrounding organisms. These results confirm the differences between sites, as observed in other figures (Fig. 6 and Fig. 7). Furthermore, the index provides additional consistent information for several organisms, such as macroalgae, including turf algae, *Lobophora*, and *Peyssonnelia*.

It would have been interesting to compare the results concerning the preferences and avoidance of corals for organisms obtained using the Strauss Linear Selection Index (Fig. 5) with Manly's Resource Selection Ratio model, as these two models share similar objectives. Manly's model examines an organism's preference for using resources or habitats in its environment (resource selectivity) as a function of their availability (Manly et al. 2002; Calenge, 2006), which could also be relevant to this study if we consider the coral as the 'organism' and the CCAs as the 'resource'. An adaptation of this model to a study similar to this one, using presence/absence data instead of the percentages required to construct the Strauss Linear Selection Index, could be envisaged.

The MDS (Multidimensional Scaling) (Arnold and Steneck., 2011) with the Bray-Curtis index could have been a good way to visualize the differences between sites. However, the number of transects conducted was not substantial enough to yield a treatable and realistic result. The graph has been created and is available in the appendix (Fig. S12). With more data and sites, this dispersion analysis would allow us to observe if the sites have significant differences in terms of recruitment as well as interactions and associations.

5. Conclusion

The aim of this study was to explore natural patterns of association between crustose coralline algae (CCAs) and corals, and to examine interactions between corals and other benthic organisms on the reefs of Moorea, French Polynesia.

A significant difference between non-cryptic and cryptic crustose coralline algae was widely observed on the reefs studied. Non-cryptic coralline algae formed mainly neutral associations with corals, some being totally neutral in their interactions, except for *P.onkodes* which showed some negative interaction results. In contrast, cryptic coralline algae showed significantly more positive responses in their relationships with coral recruits, particularly at the Temae site, where many positive associations were recorded compared to Rotui. This was particularly the case for CCA species forming thin crust, which showed positive outcomes with small (5 mm) recruits (Fig. 5), but also strong results of positive interactions (Fig. 7).

Regarding macroalgae, the results indicated a generally negative trend, especially concerning the genus *Lobophora*, observed to have very negative interactions outcome with corals. These macroalgae employ various negative mechanisms on corals, such as coral overgrowth, light obstruction, and the production of harmful secondary metabolites (Longo, 2016). However, an exception was noted with the mainly cryptic non-calcifying macroalga Peyssonnelia, which showed numerous positive associations with corals, with no negative interaction outcome recorded. This finding sets Peyssonnelia apart from the other algae studied.

The analyses revealed that negative interactions with the majority of the studied organisms were more pronounced at the Rotui site, which suggests that the degraded state of the reef has an impact on these relationships. This degradation is linked to multiple direct and indirect disturbances, primarily coral bleaching, *Acanthaster planci* outbreaks, and overfishing, which have led to massive coral losses on Moorea's reefs (Fig. S2 and S3). Consequently, these disturbances lead to potential phase shifts and the proliferation of macroalgae, shifting the dominant phase from coral-dominated to macroalgal-dominated (Barott 2012, Smith 2016). This macroalgal dominance over corals and other reef organisms results in competition for space, with non-calcifying macroalgae such as *Lobophora* and turf algae being significant colonizers, especially when the reef has experienced significant disturbance. Competition is inevitably mediated by macroalgae and determines the reef's structure and composition (McCook et al., 2001).

It has been stated that measuring reef health simply by quantifying coral cover is not accurate but can give an idea of reef condition, it is necessary to rely on other organisms or even other parameters relating to resilience, such as recruitment rate, herbivory or coral growth, which are more accurate but more complex to implement (Gibson et al., 2008; Smith et al., 2016). To deal with reefs with degraded states of health, several reef management strategies have been suggested, such as increasing herbivore populations on degraded reefs, such as Rotui, as herbivores contribute to the restoration of reef ecosystems to deal with macroalgal blooms (Mumby and Harborne, 2010; Smith et al., 2010). Furthermore, in the case of CCA, these algae play an essential role in reef resilience and restoration (Harrington, 2004) by guiding coral larvae to suitable recruitment substrates. They also have the capacity to directly regulate the abundance of other reef components, especially corals, thereby altering the structure and function of the marine ecosystem through their abundance (Harrington, 2004). Additionally, coral recruitment is a fundamental process for the maintenance and restoration of reef ecosystems (Kuffner et al., 2006).

Hence, it is imperative to continue studying the patterns of association between coral recruits and CCA, as well as interactions between corals and macroalgae, in order to better protect and manage coral reefs. This understanding is crucial, especially as many questions remain unanswered. There is still much knowledge to be gained in order to preserve and establish management plans to protect these threatened marine ecosystems.

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Links to websites for photos:

-Zeiss Stemi 2000-C ZOOM 6,5 50x): https://www.fishersci.pt/
-Sola NightSea: https://www.amronintl.com/
-Garmin Etrex 10 : https://www.bergfreunde.de/
-NOAA : https://oceanservice.noaa.gov/education/tutorial_corals/media/supp_coral04b.html

7. Appendix

Figure S1: Equipment used for research, analysis and photography of study organisms (Coral reefs, CCA, Macroalgae). (A) Garmin Etrex 10 GPS. (B) Sola NightSea UV light. (C) LEICA EZ4 HD Binocular Lens. (D) Zeiss Stemi 2000-C 6,5 50x.6,5 50x ZOOM.

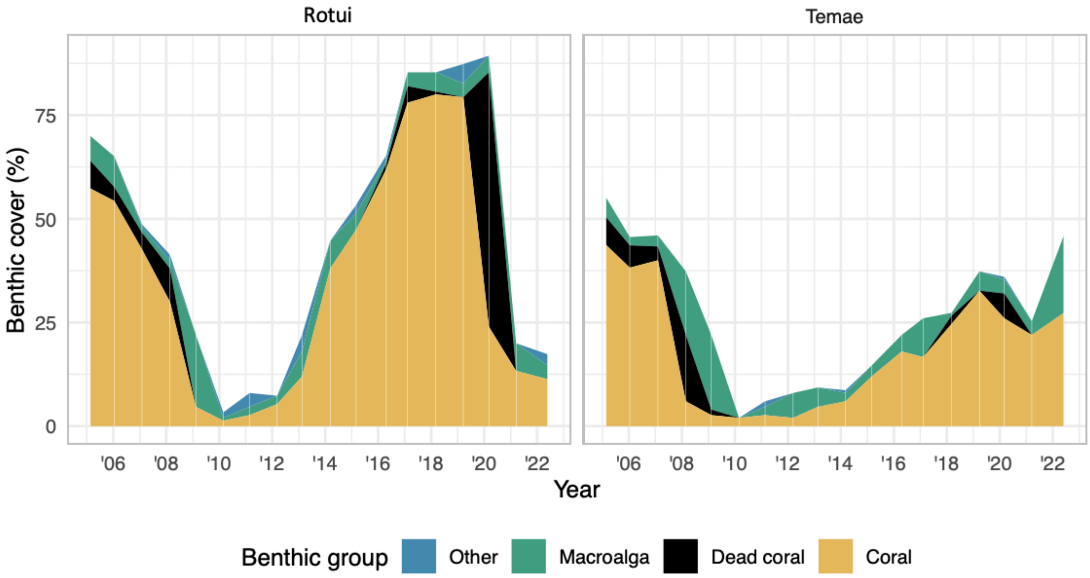

Figure S2. Percentage of Benthic cover for 4 benthic groups, Corals, Dead corals, Macroalga and Other on 2 reefs on the island of Moorea, Rotui and Temae. (Graph from Polynesia Mana (Data: Yannick Chancerelle ; Graphs: Andi Eich)).

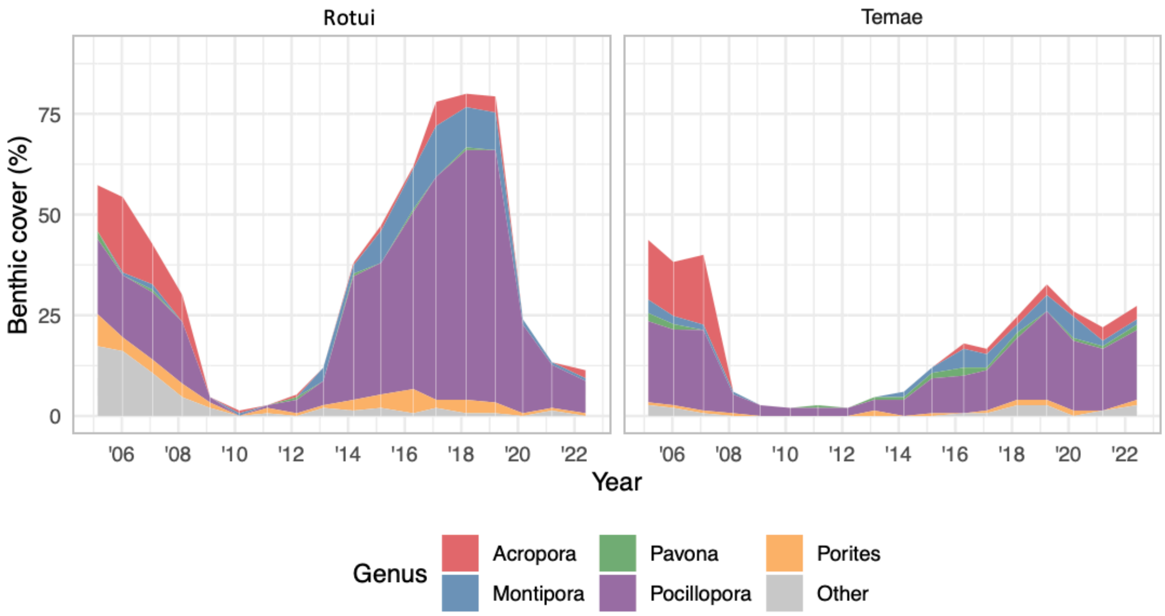

Figure S3. Percentage of the Coral benthic cover for 6 categories of genera, *Acropora*, *Montipora*, *Pavona*, *Pocillopora*, *Porites* and Other on 2 reefs on the island of Moorea, Rotui and Temae. (Graph from Polynesia Mana (Data: Yannick Chancerelle ; Graphs: Andi Eich)).

TEMAE

Quadrats	Depth (m)	Recruits number	Average size (mm) recruits per Quadrat	Average size (mm) per depth (m)	Dominant genera by quadrat
Q1	9	6	9,67	16,6	OTH
Q2		6	16,00		OTH
Q3		6	21,67		POC
Q4		3	21,25		POC
Q5	10	16	14,88	8,42	OTH
Q6	9	10	14,90	16,6	OTH
Q7	10	1	11,00	8,42	ACR
Q8		6	6,67		POC / OTH
Q9		7	12,14		OTH
Q10		3	6,67		POC
Q11		4	4,33		OTH
Q12		3	8,67		OTH
Q13		10	15,00		OTH
Q14		1	3,00		OTH
Q15		6	16,17		OTH
Q16		10	9,50		POC
Q17		7	8,00		OTH
Q18		9	6,67		ACR
Q19		6	6,50		OTH
Q20		3	4,00		ACR
Q21		12	5,25		POC
Q22		7	9,00		POC
Q23		9	3,78		POC
Q24		7	5,43		POC
Q25		10	6,60		POC
Q26		8	5,88		POC
Q27		10	3,80		OTH
Q28		8	3,80		POC
Q29		13	16,38		OTH
Q30		25	10,76		ACR
Q31		12	11,42		POC
Q32		5	11,80		OTH

Table S1. Table of Quadrats from Temae, indiquant la profondeur, le nombre de recrues par quadrat, la taille moyenne des recrues par quadrats, taille moyenne par profondeur ainsi que le genre dominant

ROTUI

Quadrats	Depth (m)	Recruits number	Average size (mm) recruits per Quadrat	Average size (mm) per depth (m)	Dominant genera by quadrat
Q1	12	5	4,80	11,15	POC
Q2		3	15,33		OTH
Q3		5	5,80		OTH
Q4		7	11,86		POC
Q5		5	15,40		OTH
Q6		5	15,20		OTH
Q7		6	14,50		OTH
Q8		2	21,50		OTH
Q9		9	9,78		OTH
Q10		8	14,75		OTH
Q11		6	6,83		ACR
Q12		8	13,88		ACR
Q13		5	11,00		ACR/POC
Q14		7	8,71		POC
Q15		11	14,45		POC
Q16		7	14,29		OTH
Q17		8	16,50		ACR
Q18		5	8,80		ACR
Q19		9	5,67		ACR/POC
Q20		4	7,50		POC
Q21		4	2,00		POC
Q22		3	6,67		POC
Q23	11	5	3,60	7,16	POC
Q24		8	7,63		POC
Q25		5	6,60		ACR/POC
Q26		6	10,83		ACR/POC
Q27	10	8	9,25	9,32	OTH
Q28		6	9,50		POC
Q29		3	5,67		POC
Q30		4	5,00		POC
Q31		3	11,00		OTH
Q32		2	15,50		OTH/POC
Q33	9	7	3,00	8,92	POC
Q34		6	8,50		OTH
Q35		4	6,75		OTH
Q36		6	9,33		OTH
Q37		5	12,60		OTH
Q38		3	13,33		ACR/POC/OTH

Table S2. Table of Quadrats from Temae, indiquant la profondeur, le nombre de recrues par quadrat, la taille moyenne des recrues par quadrats, taille moyenne par profondeur ainsi que le genre dominant

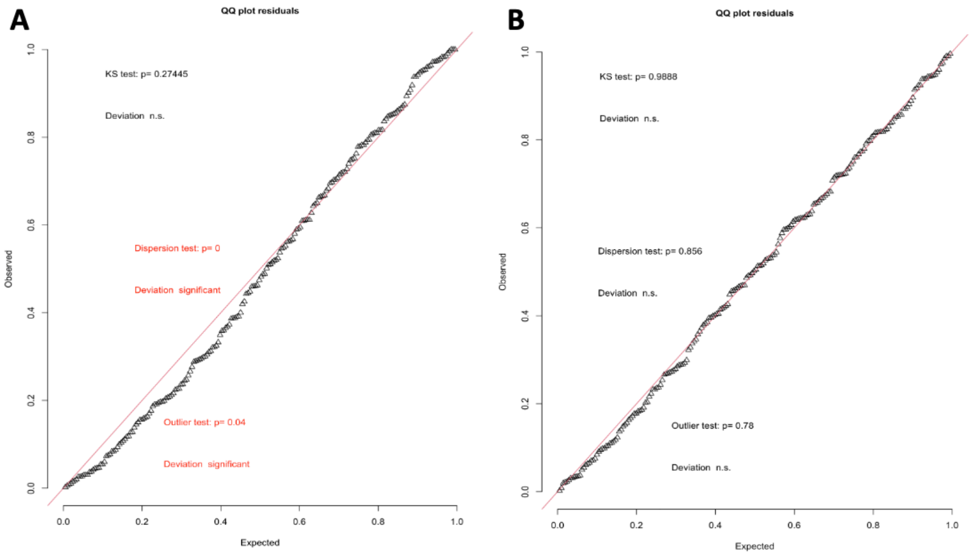

Figure S4. Poisson and Negative Binomial QQ plot residuals (DHARMA residuals)

Figure S5. *Acanthaster planci* (Kayal et al., 2012)

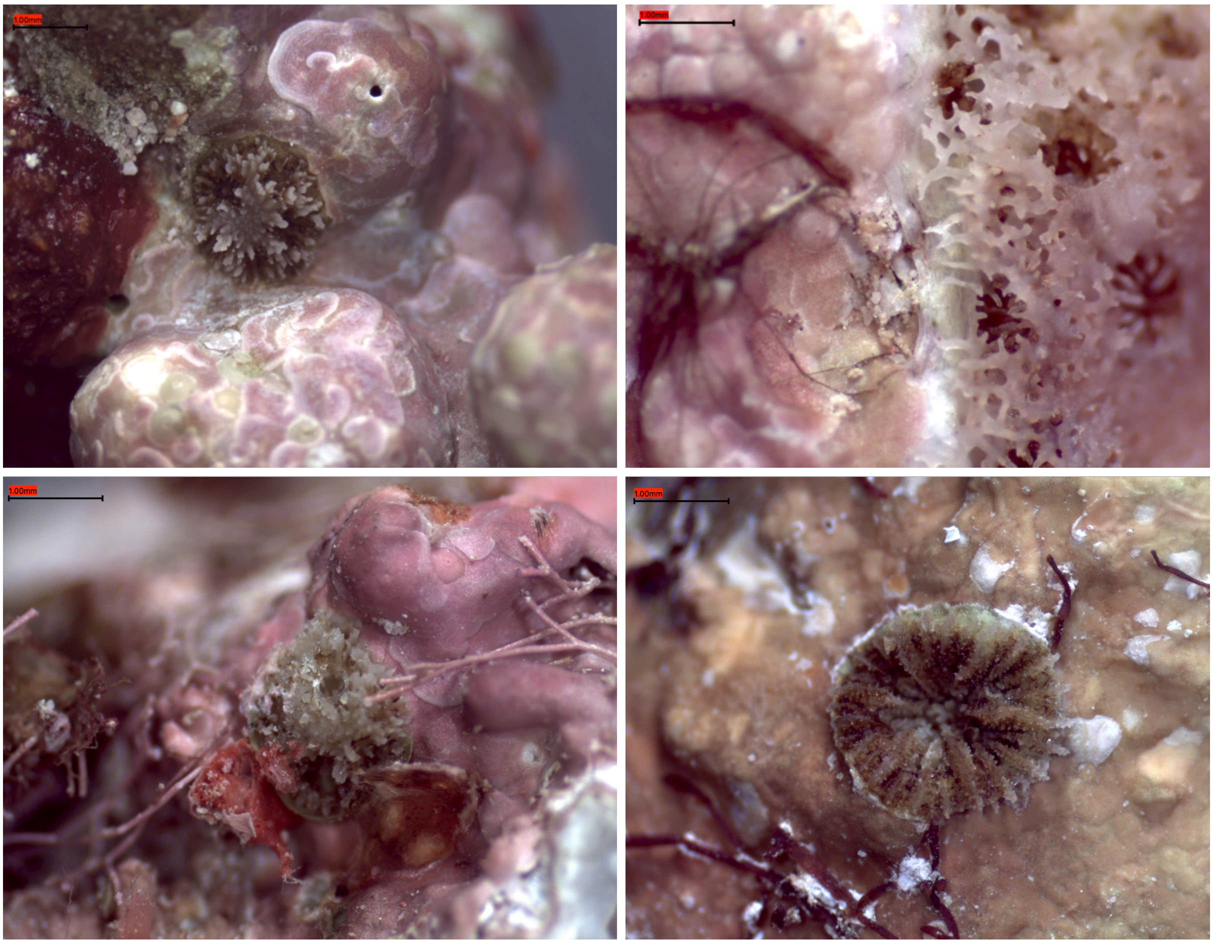

Figure S6. In Laboratory photographs representative 4 Coral-Crustose Coralline Algae associations. A) Coral growing on *Lithophyllum sp.3.* B) Coral of the genus Acropora growing on *Lithophyllum sp.3.* C) Coral of the genus Acropora growing on *Lithophyllum sp.3.* D) Coral in catégorie "Oth" growing on *Harveylithon munitum.*

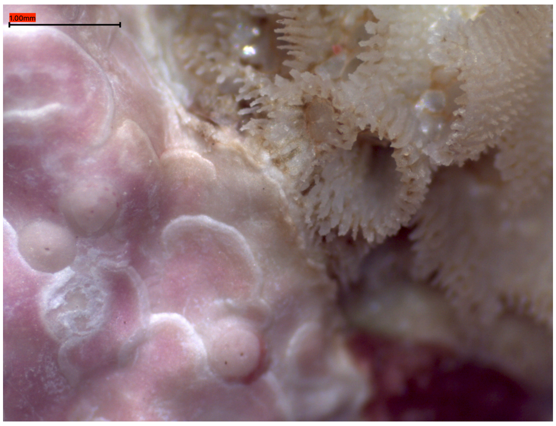

Figure S7. In Laboratory photographs showing Coral of the genus Pocillopora in neutral interaction with *Lithophyllum sp.3*

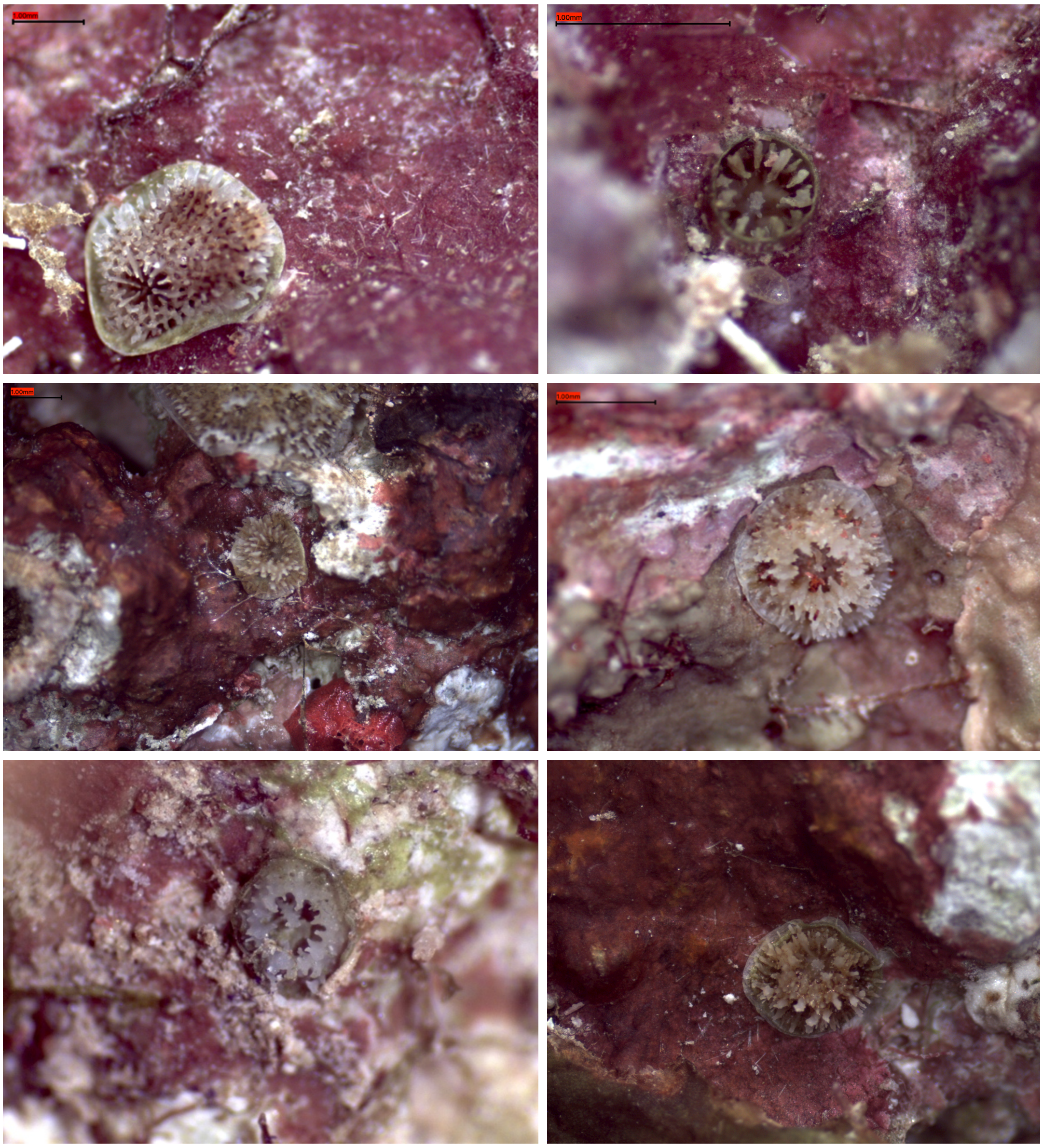

Figure S8. In Laboratory photographs representative 6 Peyssonnelia Algae in association with different coral genera. A) Acropora on Peyssonnelia. B) Acropora on Peyssonnelia. C) Pocillopora on Peyssonnelia. D) Pocillopora on Peyssonnelia.
E) Coral of the genus Porites (Oth) on Peyssonnelia (size of the coral: 1mm). F) Coral of the genus Pocillopora in interaction with Peyssonnelia (size of the coral: 1.5mm).

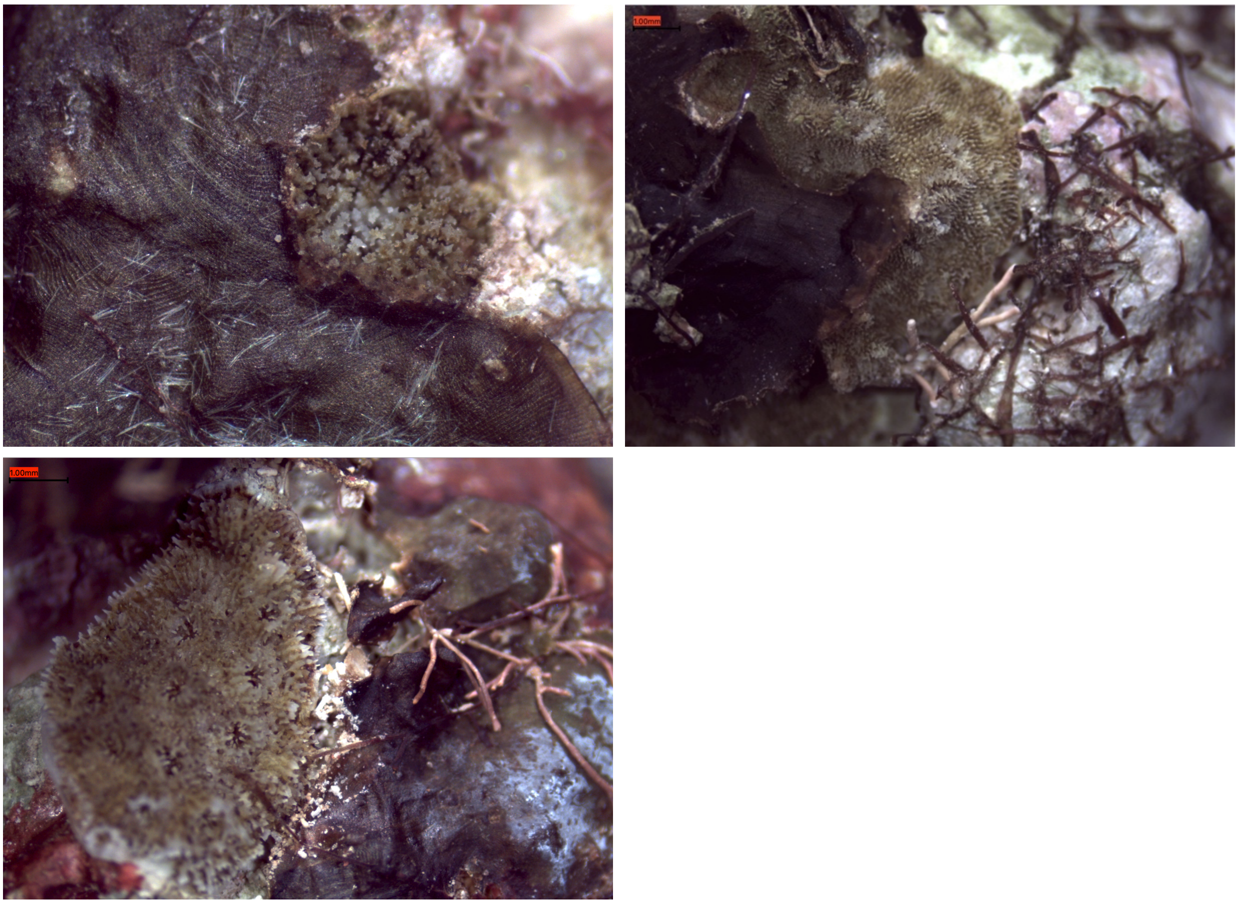

Figure S9. In Laboratory photographs showing the interaction between Corals and the Algae *Lobophora*. A) Coral of the category Other (Oth) covered by *Lobophora.* (Without scale). B) Coral of the genus Acropora covered by *Lobophora*. C) Coral of the genus Acropora in neutral interaction CCA.

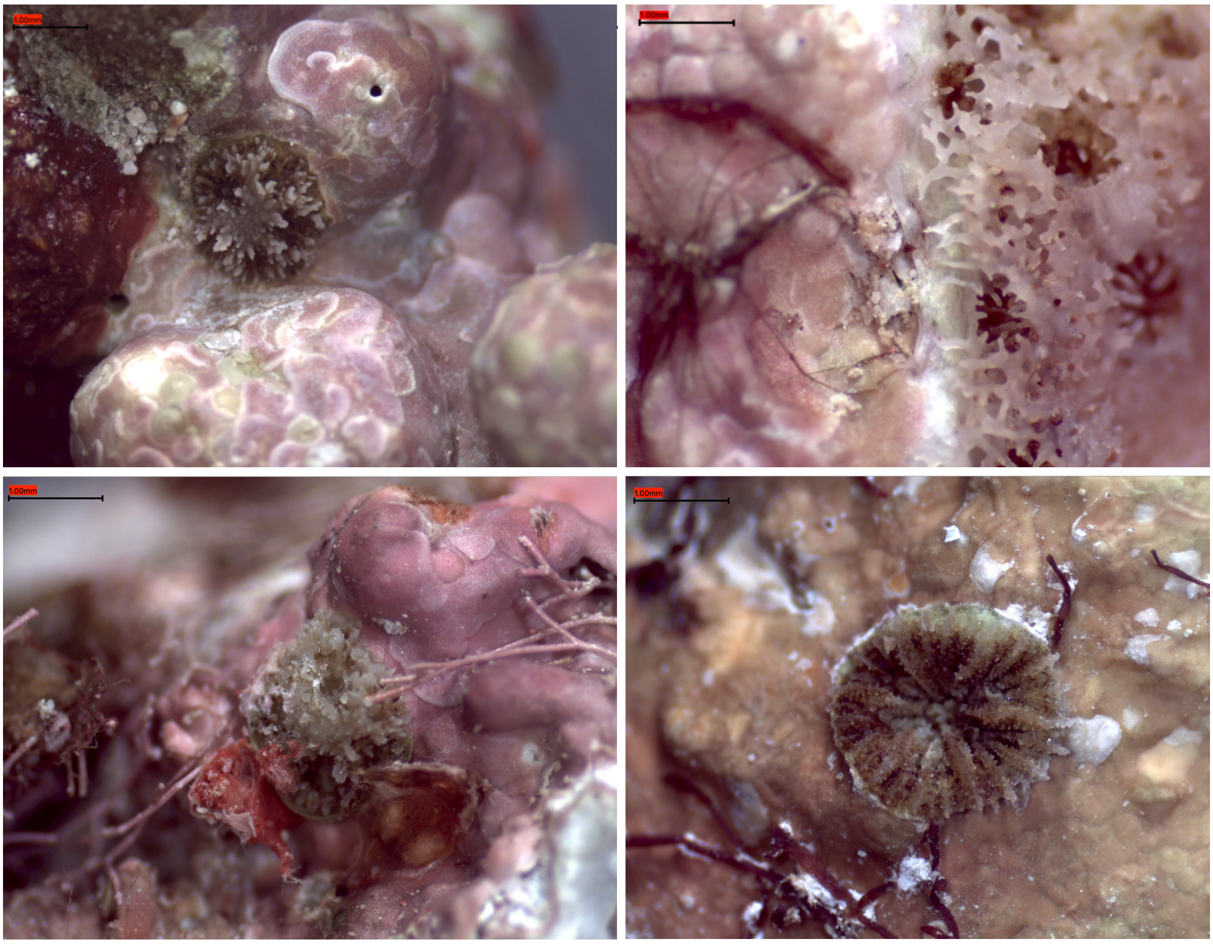

Figure S10 In Laboratory photographs representative 4 Coral-Crustose Coralline Algae associations. A) Coral growing on *Lithophyllum sp.3.* B) Coral of the genus Acropora growing on *Lithophyllum sp.3.* C) Coral of the genus Acropora growing on *Lithophyllum sp.3.* D) Coral in catégorie "Oth" growing on *Harveylithon munitum.*

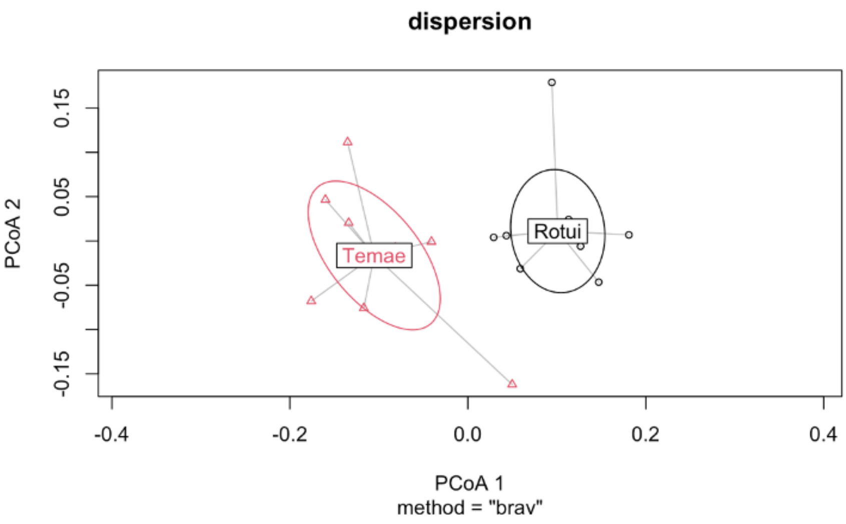

Figure S11. Dispersion plot of the Temae and Rotui sites